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PHYLOGENY OF ALLOSAUROIDEA (DINOSAURIA: THEROPODA): COMPARATIVE ANALYSIS AND RESOLUTION

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SYNOPSIS Allosauroidea, a clade of large-bodied theropod dinosaurs that ranged from the Middle Jurassic until the Late Cretaceous, has been the subject of extensive phylogenetic study. However, despite the publication of twelve cladistic analyses little phylogenetic consensus has emerged, frustrating attempts to use these dinosaurs to study character evolution, biogeography, and the quality of the fossil record. Here we analyze a core subset of allosauroids using cladistic methodology and several comparative methods. After reviewing previous studies and their points of disagreement, we present a new cladistic analysis that integrates data from these studies with new characters. This analysis finds strong support for placing *Sinraptor* as a basal allosauroid, *Neovenator* as a basal member of Carcharodontosauridae, and *Acrocanthosaurus* as a more derived member of Carcharodontosauridae, rather than the sister taxon of *Allosaurus* as sometimes advocated. The current dataset is compared in detail to those of previous studies to determine the degree of overlap and the basis for differing topologies. These comparisons show that scoring differences, character choice, and taxonomic sampling all play a major role in generating incongruence. Finally, the recovered most parsimonious topology is used to assess character evolution, stratigraphic congruence, and biogeography. This topology shows a strong overall match with the stratigraphic record,

and is much more congruent with stratigraphy than any alternative topology. The biogeographic history of core allosauroids is also strongly congruent with the breakup sequence of Pangaea.

KEY WORDS vertebrate palaeontology, evolution, cladistics, stratigraphy, palaeobiogeography, Mesozoic

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INTRODUCTION

The large-bodied Late Jurassic theropod *Allosaurus* (Figure 1) is among the best-studied dinosaur genera, represented by hundreds of specimens that have formed the basis for a wide range of research. In recent years *Allosaurus* has featured prominently in studies of palaeopathology (Hanna 2002), taphonomy and palaeoecology (Gates 2005), intraspecific variation (Chure & Madsen 1996, Smith 1998, Smith *et al*. 1999, Smith & Lisak 2001), growth and ontogeny (Rauhut & Fechner 2005, Bybee *et al.* 2006), biomechanics (Rayfield *et al.* 2001, Rayfield 2005), and biogeography (Perez-Moreno *et al.* 1999, Sereno 1999b). Over the past decade numerous phylogenetic studies have also clarified the higher-level position of *Allosaurus* among theropods. Although once allied with *Tyrannosaurus* and other large theropods (within "Carnosauria"), *Allosaurus* is now routinely recovered as a basal tetanuran, closely related to *Sinraptor*, *Carcharodontosaurus*, and *Giganotosaurus* (e.g., Holtz 1994, Sereno *et al.* 1996, Holtz 2000, Rauhut 2003, Holtz *et al*. 2004). These taxa, along with *Acrocanthosaurus*, *Neovenator*, and several new genera, comprise Allosauroidea (Table 1). Defined as a stem-based taxon, Allosauroidea comprises the most inclusive clade containing *Allosaurus fragilis* but not *Passer domesticus* (Table 2).

Although Allosauroidea is confidently placed near the base of Tetanurae, the ingroup relationships of this clade remain contentious and unresolved. While more attention has been devoted to the phylogeny of allosauroids than to nearly any other archosaur clade (twelve cladistic analyses), little phylogenetic consensus has emerged (Sereno *et al*. 1996, Harris 1998, Forster 1999, Holtz 2000, Currie & Carpenter 2000, Azuma & Currie 2000, Allain 2002, Coria & Currie 2002, Rauhut 2003, Holtz *et al*. 2004, Novas *et al*. 2005, Coria & Currie 2006). *Acrocanthosaurus* and *Neovenator* are alternatively recovered as either sister taxa to *Allosaurus* or as more closely related to *Carcharodontosaurus*, and *Sinraptor* is positioned either as the basalmost allosauroid or as the sister taxon to carcharodontosaurids. Understanding and resolving these conflicts is critical, as allosauroids are a diverse, long-lived, and geographically widespread group well-suited for studies of character acquisition, biogeography, distribution, and the

quality of the fossil record. Unfortunately, reasons for these different topologies are not immediately obvious, and are not discussed in detail in any of the published analyses. This underscores a much larger problem in the study of dinosaur phylogeny: although certain clades are subjected to a great deal of phylogenetic study, there is often little attempt to record shared data and critically compare alternative analyses.

Here we aim to analyze allosauroid phylogeny and evolutionary history using cladistic methodology and several comparative methods. First, we review previous studies and assess the current points of disagreement and consensus in allosauroid phylogeny. Next we present a new cladistic analysis that integrates data from previous studies and adds several new characters, resulting in the most expansive dataset applied to this clade. Many of these new characters, as well as revision of published characters, stem from the discovery of several new taxa (*Eocarcharia*, *Mapusaurus*, *Tyrannotitan*), description of new specimens (*Carcharodontosaurus*: Brusatte & Sereno 2005, in press), and the reanalysis of described material (*Neovenator*: Brusatte *et al*., in prep) which allow for new character scores and the discovery of new synapomorphies. Then, we extensively compare our data to those in previous studies, evaluate the degree of overlap, and attempt to identify the source for different topologies. Finally, we use our recovered topology to assess character evolution, stratigraphic congruence, and biogeography.

INSTITUTIONAL ABBREVIATIONS

BMNH, The Natural History Museum, London, England; **IVPP**, Institute of Vertebrate Palaeontology and Palaeoanthropology, Beijing, China; **MIWG**, Dinosaur Isle (Museum of Isle of Wight Geology), Sandown, England; **MNN**, Musée National du Niger, Niamey, Republique du Niger; **MUCPv-CH**, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén, Argentina; **NCSM**, North Carolina State Museum of Natural Sciences, Raleigh, North Carolina; **OMNH**, Sam Noble Oklahoma Museum of Natural History, Norman, Oklahoma; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan, San Juan, Argentina; **SGM**, The Ministere de l'Energie et des Mines, Rabat, Morocco; **UCRC**, University of Chicago Research Collection, Chicago, Illinois; **UMNH**, Utah Museum of Natural History, Salt Lake City,

Utah; **UUVP**, University of Utah, Vertebrate Paleontology Collection, Salt Lake City, Utah.

ALLOSAUROID MONOPHYLY

Allosauroidea is employed here as a stem-based taxon that encompasses all dinosaurs closer to *Allosaurus* than to birds (Table 2). The monophyly of such a taxon has been demonstrated by nearly every large-scale study of theropod phylogeny, which find support for a grouping of *Allosaurus*, *Sinraptor*, and carcharodontosaurids to the exclusion of spinosaurids, *Afrovenator*, *Torvosaurus*, and other "megalosaur-grade" taxa (Sereno *et al*. 1996, Holtz 2000, Holtz *et al*. 2004; see Rauhut [2003] for a somewhat different topology). Supporting synapomorphies include nasal participation in the antorbital fossa, invaginated recesses within the lacrimal, a dorsal boss on the postorbital, a large articular flange on the quadrate for the quadratojugal, strongly ventrally deflected paroccipital processes, and a notch between the paroccipital processes and the basal tubera. Other synapomorphies listed in the studies cited above are less secure in light of recent discoveries and reanalysis.

Despite widespread support for Allosauroidea as a clade, membership has varied because of the lack of information or completeness regarding several taxa, such as *Monolophosaurus*, *Fukuiraptor*, *Lourinhanosaurus*, *Siamotyrannus*, *Cryolophosaurus*, and *Megaraptor*. While some analyses recover one or more of these taxa nested within a stem-based Allosauroidea, others report widely varying positions (including placement within Spinosauroidea or among a nexus of basal tetanurans). Thus, we restrict the new cladistic analysis and comparisons to a suite of nine bona fide allosauroid taxa, whose status as allosauroids is supported by available character evidence and most of whose fossil remains we have been able to examine in person. A more complete comparative analysis of allosauroid monophyly and membership is currently in preparation (Brusatte *et al*., in prep).

RECENT CLADISTIC ANALYSES

Twelve published studies have analyzed allosauroid interrelationships, although each considers relationships well beyond Allosauroidea. Topologies recovered by these studies are shown in Figure 2, with only the allosauroid terminal taxa shown. Basic descriptive statistics for each study are provided in Table 3, including the number of informative characters applicable to Allosauroidea. A strict consensus tree of these studies lacks any structure (Figure 2L), and clearly demonstrates that there is little agreement regarding allosauroid interrelationships.

All analyses recovered a monophyletic Allosauroidea, with the exception of Forster (1999), who found allosauroids as a paraphyletic grade relative to *Tyrannosaurus*, the representative coelurosaur in the analysis. In the other studies, Allosauroidea usually includes three family-level taxa: Sinraptoridae, Allosauridae, and Carcharodontosauridae. Phylogenetic definitions of these taxa are provided in the Phylogenetic Taxonomy section below, as well as in Table 2.

The interrelationships of Sinraptoridae are not considered by most studies. Although *Sinraptor* and *Yangchuanosaurus* are often referred to this taxon, the species *Sinraptor dongi* is the best described and most often coded, either as a species or a representative of the family. Several analyses (e.g., Sereno *et al*. 1996, Currie & Carpenter 2000, Rauhut 2003, Holtz *et al*. 2004, Coria & Currie 2006) recovered a polytomy of *Sinraptor*, Allosauridae, and Carcharodontosauridae (and sometimes other taxa). Forster (1999) placed *Sinraptor* as the sister taxon to a novel *Allosaurus* + *Tyrannnosaurus* clade, but no other studies found a grouping of Allosauridae and *Sinraptor* to the exclusion of other allosauroids. Some studies (Coria & Currie 2002, Allain 2002) placed *Sinraptor* as the sister group to Carcharodontosauridae. Reanalysis of the data presented by Novas *et al*. (2005) also supports this pairing, although the published cladogram shows a different topology. Finally, other studies (Harris 1998, Holtz 2000) recovered *Sinraptor* as the basalmost allosauroid, a position concordant with stratigraphy.

Carcharodontosauridae includes *Carcharodontosaurus* and *Giganotosaurus*, as well as several taxa described recently. Of these new discoveries, only the South American *Tyrannotitan* and *Mapusaurus* have appeared in previously-published analyses

(Novas *et al*. 2005 and Coria & Currie 2006, respectively). Only Forster (1999) failed to recover a monophyletic grouping of *Carcharodontosaurus* and *Giganotosaurus*, positioning them instead as successive outgroups to a clade of *Sinraptor*, *Allosaurus*, and *Tyrannosaurus*. All other analyses found these large-bodied genera as more closely related to each other than either is to *Allosaurus*, *Acrocanthosaurus*, or *Sinraptor*, but considerable disagreement persists regarding the placement of *Acrocanthosaurus* and *Neovenator*.

Acrocanthosaurus, from the Aptian-Albian of North America, was once allied with tyrannosaurids (Bakker *et al*. 1988) but is now regarded as an allosauroid. Initial analyses of allosauroid phylogeny recovered *Acrocanthosaurus* as a close relative of *Carcharodontosaurus* and *Giganotosaurus* (Sereno *et al*. 1996, Harris 1998, Holtz 2000), and thus more closely related to these taxa than to *Allosaurus*. While this placement was corroborated by the large-scale analysis of Holtz *et al*. (2004) and assumed by Rauhut (2003), several recent studies found *Acrocanthosaurus* to be the sister taxon to *Allosaurus* (e.g., Currie & Carpenter 2000, Allain 2002, Novas *et al*. 2005, Coria & Currie 2006). Although their analysis did not recover this exact topology, Coria & Currie (2002) found support for a (*Sinraptor* (*Carcharodontosaurus* + *Giganotosaurus*)) grouping to the exclusion of *Acrocanthosaurus*, based primarily on braincase characters. Many of these latter authors dismissed as size-related several characters used by Sereno *et al*. (1996) and Harris (1998) to link *Acrocanthosaurus* and more derived carcharodontosaurids.

Neovenator, a relatively recent discovery from the Barremian of England (Hutt *et al*. 1996, Naish *et al*. 2001), has been included in four analyses (Harris 1998, Holtz 2000, Rauhut 2003, Holtz *et al*. 2004). Despite its relative completeness and the publication of new illustrations (Naish *et al*. 2001), *Neovenator* has been ignored in many recent analyses. Although originally described as closely related to *Allosaurus* (Hutt *et al*. 1996), *Neovenator* is recovered as an allosaurid only by Holtz (2000). The analyses of Harris (1998), Rauhut (2003), and Holtz *et al*. (2004) each found *Neovenator* as more closely related to *Carcharodontosaurus* than to *Allosaurus*, and hence a member of Carcharodontosauridae.

Relationships within Allosauridae are not considered by most analyses. Indeed, if *Acrocanthosaurus* and *Neovenator* are closer to *Carcharodontosaurus* than to *Allosaurus*, and if *Saurophaganax* is nothing more than a large species of *Allosaurus* (Smith 1998), then *Allosaurus* may be the only included genus and is thus redundant with the family (see review in Chure [2000]).

As a final note, the analysis of Azuma & Currie (2000) only includes *Allosaurus*, *Acrocanthosaurus*, and *Sinraptor* as terminal taxa, and thus cannot adequately test the conflicting positions of *Sinraptor* and *Acrocanthosaurus* discussed above.

In summary, although 12 cladistic analyses have examined allosauroid relationships, little consensus has emerged. The only ingroup node with significant support is the *Carcharodontosaurus* + *Giganotosaurus* sister grouping. The placement of *Sinraptor*, *Acrocanthosaurus*, and *Neovenator* remain unresolved, and little attempt has been made to understand this incongruence.

NEW CLADISTIC ANALYSIS

A new phylogeny of Allosauroidea is presented here, based on a matrix of characters culled from previous phylogenetic analyses, as well as several new characters. Details on taxon selection, outgroups, character choice, and missing data are presented below, and the character list (Appendix 1) and data matrix (Appendix 2) are included at the end of this paper, while a synapomorphy list is included in the supplementary information (Supplementary Appendix 1).

Materials and Methods

Nine ingroup taxa and four outgroups were scored for 99 morphological characters. The data matrix was created in MacClade 4.06 (Maddison & Maddison 2003) and analyzed using PAUP* v.4.0b10 (Swofford 2000). A branch-and-bound search generated a single most parsimonious tree (MPT), which is discussed in the Results section below. The robustness of individual clades was assessed using two tree-support measures: the bootstrap (1000 replicates) and Bremer support (decay indices).

Ingroup Selection. The nine selected ingroup taxa include: *Acrocanthosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Eocarcharia*, *Giganotosaurus*, *Mapusaurus*, *Neovenator*, *Sinraptor*, and *Tyrannotitan*. These comprise the best known and previously-analyzed allosauroids, based on a number of higher-level analyses of theropod phylogeny (Sereno *et al*. 1996, Sereno 1999a, Holtz 2000, Rauhut 2003, Holtz *et al*. 2004, Sereno & Brusatte in press). Taxa less consistently regarded as allosauroids (e.g., *Afrovenator*, *Cryolophosaurus*, *Fukuiraptor*, *Lourinhanosaurus*, *Monolophosaurus*, *Siamotyrannus*) are excluded, as they are better analyzed in the context of a broader selection of basal tetanurans. However, as a heuristic tool we have provisionally coded *Monolophosaurus* and *Fukuiraptor* for our character list, as discussed below.

Although Sinraptoridae is often coded as a single terminal taxon in other analyses, several problems have been identified with the use of higher-level terminal taxa in phylogenetic studies (Binida-Edmonds *et al*. 1998). Thus, we have elected to code the genus *Sinraptor* as a representative for sinraptorids, based on our examination of original material (IVPP 10600) and its well-documented morphology (Gao, 1992; Currie & Zhao, 1993). We exclude *Yangchuanosaurus*, as although one of us (PCS) has examined some of the material first-hand, published descriptions are incomplete (e.g., Dong *et al*., 1978, 1983), and this taxon appears to be extremely similar to *Sinraptor* in overall morphology (Rauhut 2003). We also exclude *Saurophaganax*, as its generic status is controversial (Smith 1998), the known material is fragmentary and poorly-preserved (Chure 1995, 2000), and this taxon appears to be extremely similar to *Allosaurus* in overall morphology (SLB, pers. ob.).

Acrocanthosaurus, *Allosaurus*, *Carcharodontosaurus*, *Eocarcharia*, *Giganotosaurus*, *Neovenator*, and *Sinraptor* were scored based on first-hand observations, as well as published reports. *Mapusaurus* and *Tyrannotitan* were scored based on published reports. A full list of scoring sources is provided in Appendix 3.

Outgroup Selection. Based on several higher-level analyses of theropod phylogeny (Sereno 1999a, Holtz 2000, Rauhut 2003, Holtz *et al*. 2004), four outgroups (*Herrerasaurus*, *Coelophysis*, *Torvosaurus*, Compsognathidae) were chosen to determine character polarity. These taxa are well-known representatives of Herrerasauridae,

Coelophysoidea, Spinosauroidea, and basal coelurosaurians, respectively, which represent important, successively more closely related, outgroups to Allosauroidea. Furthermore, these particular outgroups were selected to represent the presumed ancestral condition of Theropoda, Neotheropoda, Tetanurae, and Coelurosauria, respectively. Choosing a taxon to represent the primitive coelurosaur bauplan is not trivial, as many basal coelurosaur groups (tyrannosauroids, ornithomimids, alvarezsaurids) are significantly derived, and often possess a highly autapomorphic morphology. Although one recent analysis (Hwang *et al*. 2004) recovered compsognathids as more derived than tyrannosauroids and ornithomimids, we feel that Compsognathidae best encompasses primitive coelurosaur morphology. While the use of higher-level terminal taxa can be problematic, Compsognathidae is demonstrably monophyletic (Hwang *et al*. 2004), and codings based on several taxa (*Compsognathus*, *Sinosauropteryx*, *Huaxiagnathus*, and *Mirischia*) compensate for fragmentary specimens and incomplete illustrations and descriptions. Additionally, there are no demonstrable polymorphisms for the characters in this analysis. In the future, several recently-discovered basal tyrannosauroids (Hutt *et al*. 2001, Xu *et al*. 2004, Xu *et al*. 2006, Sereno & Brusatte in prep) may provide a more accurate basal coelurosaur outgroup free from the assumptions employed here, but the anatomy and relationships of these taxa are still poorly understood (Sereno & Brusatte submitted).

Selecting a basal tetanuran outgroup is also difficult, as *Afrovenator*, and *Dubreuillosaurus*, *Torvosaurus*, and spinosaurids are exceedingly incomplete and/or only briefly described in the literature. Although it can only be scored for 51 of our characters (52%), *Torvosaurus* was employed as an outgroup over other spinosauroids that remain relatively less well documented.

Herrerasaurus was scored based on our own observations, while *Coelophysis*, *Torvosaurus*, and Compsognathidae were primarily scored from published descriptions and figures, as well as casts.

Character Choice. Taxa were scored for 99 morphological characters, 21 of which are new to this study. Other characters were culled from the literature, and every published character informative for allosauroid phylogeny was considered. Although an attempt

was made to use all previous character data that remained informative, some characters were dismissed if they: (1) were poorly defined or could not be sufficiently quantified, (2) exhibit overlapping variation that cannot be separated in ingroup and outgroup taxa, (3) were redundant with other characters, or (4) were only informative at the level of Allosauroidea due to scoring mistakes (see Supplementary Appendix 3). Original authorship of all characters is shown after the character in Appendix 1. Polarity was determined by reference to the outgroups, whose relationships were constrained based on published analyses of theropod phylogeny (Sereno *et al*. 1996, Sereno 1999a, Holtz 2000, Holtz *et al*. 2004). Most of the characters are binary, although five are multistate, all of which were left unordered. These characters include 59 (60%) cranial characters, 16 (16%) axial characters, and 24 (24%) appendicular characters.

New Characters. The 21 new characters (10 cranial, 2 axial, 9 appendicular), comprising 21% of the dataset. The primitive and derived states of most of these characters are illustrated (Figures 3, 4).

Four new characters (50-53) concern the dentary, and came to light during the description of a partial dentary of *Carcharodontosaurus* (Brusatte & Sereno 2005, in press). Derived states include a distinct ventral dentary flange ("dentary chin"), a principal row of neurovascular foramina that curves ventrally as it extends posteriorly, external texturing, and a marked angle between opposing dentaries at the symphysis, each of which is scored for several carcharodontosaurids. Additionally, two new characters concern the gastralia: a medial gastral element that expands distally into a club-shaped prominence (74) and multiple sets of fused medial elements (75). Reexamination of allosauroid tibiae revealed two additional derived states shared by some carcharodontosaurids: an elongated and expanded medial malleolus (90) and a distally expanded lateral malleolus (91). Finally, the recently-described *Mapusaurus* shares with *Acrocanthosaurus* metacarpals with greatly expanded proximal articular surfaces (99).

Missing Data. Missing data range from 0% (*Allosaurus*) to 80% (*Tyrannotitan*) (Table 4). *Sinraptor* and *Acrocanthosaurus* both have less than 10% missing data, while *Eocarcharia* and *Mapusaurus* have more than 50%. The total missing data in this 9 x 99

matrix is 35%. Missing data is not concentrated in any one anatomical region, as some taxa are known from little skull material (e.g., *Tyrannotitan*), whereas others are represented by few postcranial elements (e.g., *Carcharodontosaurus*, *Eocarcharia*). Although large amounts of missing data can substantially increase the number of MPTs, taxa with large amounts of missing data are here included for completeness (Kearney & Clark 2002), as no terminals taxa fulfill Wilkinson's (1995) criteria for safe taxonomic reduction.

Results

With outgroups constrained, the analysis yielded a single most parsimonious tree with a length of 171 steps, a consistency index (CI) of 0.61, and a retention index (RI) of 0.70 (Figure 5). *Sinraptor* is recovered as the most basal allosauroid taxon, with *Allosaurus* and Carcharodontosauridae successively more derived. Every terminal taxon in the analysis, with the exception of *Sinraptor* and *Allosaurus*, belongs to Carcharodontosauridae by definition (Table 2; see section on Phylogenetic Taxonomy) below. Within Carcharodontosauridae, *Neovenator* is recovered as the most basal member of the group, followed successively by *Tyrannotitan*, a clade comprised of *Acrocanthosaurus* and *Eocarcharia*, a clade comprised of *Giganotosaurus* and *Mapusaurus*, and *Carcharodontosaurus*. A list of synapomophies, as optimized under accelerated (ACCTRAN) and derived (DELTRAN) transformation assumptions, is presented in Supplementary Appendix 1.

Tree Support Measures. Robustuness was assessed with bootstrap (1000 replicates) and Bremer support (decay) indices (Figure 5). Both methods were chosen to give a more complete description of clade robustness, as problems have been identified with each method (Kitching *et al*. 1998). All ingroup nodes except for the *Giganotosaurus* + *Mapusaurus* node have a Bremer support value greater than one—that is, they still appear in the strict consensus of all trees up to one step longer than the MPT. The highest decay indices are exhibited by Carcharodontosauridae and the *Allosaurus* + Carcharodontosauridae node, which collapse five steps out from the MPT. All other nodes have decay indices of two. Not surprisingly, high bootstrap values are also seen at

the *Carcharodontosaurus* + *Giganotosaurus* node (91%), Tyrannotitan + derived carcharodontosaurids node (80%), Carcharodontosauridae node (90%), and *Allosaurus* + Carcharodontosauridae node (84%).

Alternative Topologies. Constraining tree topology in PAUP* allows for the examination of alternative topologies, as well as the cost required to assume these topologies. An *Acrocanthosaurus* + *Allosaurus* grouping to the exclusion of carcharodontosaurids, as hypothesized by many studies (e.g., Currie & Carpenter 2000, Allain 2002, Coria & Currie 2002, Novas *et al*. 2005; Coria & Currie 2006) requires an additional 27 steps, or 16% of the length of the MPT. A sister group relationship between *Allosaurus* and *Neovenator*, as found by Holtz (2000), requires an additional five steps. Placing *Sinraptor* as the sister group to carcharodontosaurids requires eight additional steps.

Taxon Removal. Although ingroup taxa with high amounts of missing data were not deleted from the initial analysis, several fragmentary terminal taxa were excluded to observe any effect on tree topology (Figure 6). Deletion of *Eocarcharia* (69% missing data) and *Tyrannotitan* (80% missing data) did not affect tree topology. However, deletion of *Neovenator* (44%) results in four MPTs, the strict consensus of which recovers *Acrocanthosaurus*, *Eocarcharia*, *Tyrannotitan*, and Carcharodontosaurinae (*Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus*) in a polytomy at the base of Carcharodontosauridae. Thus, the current analyis is somewhat sensitive to taxon selection, and *Neovenator* appears to be a particularly crucial taxon for resolving carcharodontosaurid interrelationships.

Additional Taxa. Although *Fukuiraptor* and *Monolophosaurus* are not recovered as allosauroids in all higher-level analyses of theropod phylogeny (see above), they were scored to examine any effects they may have on tree topology (Appendix 2). When *Fukuiraptor* and *Monolophosaurus* are included in the analysis five MPTs result (TL=180, CI=0.58, RI=0.69), the strict consensus of which collapses *Allosaurus*, *Fukuiraptor*, *Monolophosaurus*, and Carcharodontosauridae into a polytomy more derived than *Sinraptor*. Other than the creation of this polytomy, tree topology does not

change. However, it must be noted that all characters were selected to be informative among the nine original ingroups, without reference to *Monolophosaurus* and *Fukuiraptor* during the character selection process. Since basal tetanuran characters and ingroups are not included in the present analysis, and due to high amounts of missing data (due to fragmentary specimens and/or brief literature descriptions), these placements should be regarded as tentative. What is significant is that inclusion of these two potential basal allosauroids does not change the relative topology of the nine original terminal taxa.

COMPARATIVE CLADISTICS

The new cladistic analysis presented herein is the thirteenth such study to examine allosauroid interrelationships. As described above, previous studies have produced numerous different topologies, due largely to the widely varying positions of *Sinraptor*, *Acrocanthosaurus*, and *Neovenator*. This problem is not unique to Allosauroidea, as the widespread use of cladistics over the past two decades has produced copious alternative phylogenetic hypotheses for many clades. Unfortunately, in the dinosaur literature, little attempt has been made to carefully enumerate the similarities and differences between studies, and critically examine why alternative analyses produce differing results. Often, differing topologies are noted and compared, but little effort is expended to determine the root causes underlying different results. As Allosauroidea is a relatively small clade that has received much phylogenetic attention, it is well suited for a more thorough examination of cladogram incongruence.

We compare our results with those of Currie & Carpenter (2000), Allain (2002), and Novas *et al*. (2005). These analyses are chosen because their topologies differ most substantially from that of the current analysis. Other analyses (e.g., Sereno *et al*. 1996, Harris 1998, Rauhut 2003, Holtz *et al*. 2004) largely agree with the current study, whereas those of Forster (1999) and Azuma & Currie (2000) contain too few allosauroid taxa for extensive comparison. The 15-character analysis of Coria & Currie (2002) also produces a much different topology, but most of their characters are utilized by Novas *et al*. (2005). Additionally, the analysis of Coria & Currie (2006) uses the character list and

data matrix of Currie & Carpenter (2000), and thus is not considered separately. Although it is not fully critiqued, the analysis of Holtz (2000) is briefly discussed at the end of this section. In the following discussion, character numbers in parentheses refer to those in the original dataset under discussion, unless otherwise noted.

Currie & Carpenter 2000

When condensed into a set of shared taxa, the topology presented here agrees with that of Currie & Carpenter (Figure 2) in only one aspect: the sister-group relationship between *Carcharodontosaurus* and *Giganotosaurus*. Whereas *Acrocanthosaurus* is recovered as a carcharodontosaurid here, Currie & Carpenter (2000) place it as the sister taxon to *Allosaurus* (albeit with a low bootstrap support of 37% and a Bremer support of 1). Furthermore, *Sinraptor*, Carcharodontosauridae, and their Allosauridae form a polytomy. In the current analysis, *Sinraptor* falls out as the most basal allosauroid. Since the relationships of *Sinraptor* are unresolved in Currie & Carpenter's (2000) study, here we focus on the position of *Acrocanthosaurus*, whose sister-group relationship with *Allosaurus* is supported by nine synapomorphies in their analysis. These are discussed individually below.

Antorbital Openings: *Acrocanthosaurus* and *Allosaurus* were united by the possession of a promaxillary and maxillary fenestra (character 3). However, *Giganotosaurus* was incorrectly scored as possessing only a promaxillary fenestra. The holotype maxilla (MUCP-v-CH-1) has both a large, laterally-facing maxillary fenestra and a smaller, slit-shaped promaxillary fenestra.

Basal Tubera: *Acrocanthosaurus* and *Allosaurus* were scored as having basioccipitals that do not participate in the basal tubera (character 24). This character has a long history in studies of theropod phylogeny, and was used in the analyses of Sereno *et al*. (1996), Harris (1998), Forster (1999), Holtz (2000), Azuma & Currie (2000), Allain (2002), and Novas *et al*. (2005). However, rampant scoring differences exist among these studies, especially concerning *Sinraptor* and *Acrocanthosaurus*. Rauhut (2003:55) heavily modified the wording of this character, and his more explicit language was followed by Holtz *et al*. (2004) and this study. The character employed in this study (character 46 herein) only scores *Allosaurus* and *Sinraptor* as possessing the derived state

(a basal tubera subdivided into a medial part entirely formed by the basioccipital and a lateral part formed by the basisphenoid). *Acrocanthosaurus* and *Carcharodontosaurus* are scored for the primitive state.

Paroccipital Processes: Currie & Carpenter (2000, character 26) scored *Acrocanthosaurus* and *Allosaurus* as possessing downturned paroccipital processes, the distal ends of which are located below the foramen magnum. *Carcharodontosaurus*, *Giganotosaurus*, and *Sinraptor* are scored for moderately-downturned processes. This character has also been used by several authors, but analysis of new material of *Carcharodontosaurus* (Figure 7C; Brusatte & Sereno 2005, in press), as well as reexamination of the holotype of *Sinraptor* (IVPP 10600; Currie & Zhao 1993: Fig 3, 7), suggest that highly downturned paroccipital processes are a more general allosauroid character, and likely a synapomorphy of Allosauroidea.

Carotid Opening: *Acrocanthosaurus* and *Allosaurus* were scored for a pneumatized internal carotid artery opening (character 29), a character state also seen in many coelurosaurs. While this character has also been used in many previous analyses, examination of ingroup and outgroup braincase material reveals only slight differences among taxa. We feel that this character is too variable and poorly defined to accurately score.

Haemal Arches: Currie & Carpenter (2000, character 64) scored *Acrocanthosaurus* and *Allosaurus* for haemal arches with paired anterior and posterior processes at their base. *Carcharodontosaurus* was scored for the primitive state, whereas *Giganotosaurus* and *Sinraptor* were scored "?." As unequivocal haemal arches are not known for *Carcharodontosaurus*, this taxon must be scored "?." Although still synapomorphic for *Allosaurus* and *Acrocanthosaurus*, missing data now render this character ambiguous.

Scapulocoracoid Notch: *Acrocanthosaurus* and *Allosaurus* were scored for the presence of a distinct notch between the scapular acromion process and the coracoid, while *Carcharodontosaurus*, *Giganotosaurus*, and *Sinraptor* were scored "?" (character 68). Reexamination of the holotype (MUCP-v-CH-1) and published figures (Calvo 1999: Fig 14) confirm that *Giganotosaurus* also possesses this notch, and reexamination of the holotype and published figures (IVPP 10600; Currie & Zhao 1993: Fig 20, Gao 1992: Fig

4) indicate that *Sinraptor* does not. With these changed scores, this character is now diagnostic of a more inclusive clade.

Metacarpal 4 and Mandibular Fenestra: While *Acrocanthosaurus* and *Allosaurus* are united to the exclusion of *Sinraptor* by the loss of metacarpal 4 (character 79) and a reduced external mandibular fenestra (character 38), missing data in *Carcharodontosaurus* and *Giganotosaurus* render these synapmorphies ambiguous.

Cranial Nerve V: *Acrocanthosaurus* and *Allosaurus* were scored for a fully separated trigeminal nerve foramen, while *Sinraptor* and *Carcharodontosaurus* were scored for an incipiently-divided foramen (character 28); *Giganotosaurus* was scored "?," but Coria & Currie (2002) later described an undivided trigeminal foramen in this taxon. The score for *Acrocanthosaurus* was based on the NCSM 14345 (Currie, personal communication), but the holotype braincase (OMNH 10146) shows a single, undivided foramen (Franzosa & Rowe 2005: Fig 1, 2). Similar variation is seen in *Carcharodontosaurus*: *C. saharicus* (SGM-Din 1) characterized by a single foramen and *C. iguidensis* (Brusatte & Sereno 2005, in press) possesses an incipiently-divided foramen (Figure 7A,B). In light of this variation, we do not consider this character to be informative, and reject it here.

This brief discussion of characters makes it clear that many scoring differences exist between Currie & Carpenter's (2000) analysis and our study. In fact, among the 34 characters shared between the two analyses, there are 30 scoring differences (Supplementary Appendix 2). Nineteen of these differences involve positive scores (i.e., involve more than simply a change to or from a missing datum). To observe the effect of these scoring differences, we rescored Currie & Carpenter's (2000) matrix to include the 30 scores favoured by our analysis. Analyzing this matrix in PAUP* produced a single most parsimonious tree of length 235 (CI=0.61, RI=0.58), compared to two MPTs of length 224 in the original study. This tree (Figure 8A) places *Acrocanthosaurus* as the sister taxon to a *Carcharodontosaurus* + *Giganotosaurus* clade, a placement found in our analysis but not the original study of Currie & Carpenter (2000). This suggests that scoring differences are a major source of incongruence between the topology of Currie & Carpenter (2000) and that presented here.

Additionally, the present analysis and that of Currie & Carpenter (2000) differ greatly in the number and use of informative characters. Currie & Carpenter (2000) include 35 characters informative at the level of Allosauroidea, whereas the present analysis uses 99 characters. In the present analysis, 34 of the 99 characters (34%) were also used by Currie & Carpenter (2000). Furthermore, the present analysis includes only 21 of the 35 informative characters used by Currie & Carpenter (2000), or about 60% of their data (for a list of rejected characters, see Supplementary Appendix 3). Four of these rejected characters are synapomorphies of *Allosaurus* + *Acrocanthosaurus* in the analysis of Currie & Carpenter (2000); these characters (numbers 26, 28, 29, and 64 in the original study) are discussed above. Of the remaining rejected characters, two unite all allosauroids to the exclusion of *Sinraptor* (30, 95); two unite *Acrocanthosaurus*, *Allosaurus*, and *Sinraptor* (62, 100); one unites *Acrocanthosaurus* and *Sinraptor* (16); two unites *Giganotosaurus* and *Carcharodontosaurus* (23,42); and the others are ambiguous due to missing data (27, 46, 85). Finally, the analysis of Currie & Carpenter (2000) does not include several characters linking *Acrocanthosaurus*, *Carcharodontosaurus*, and *Giganotosaurus* used in this analysis.

The present analysis and that of Currie & Carpenter (2000) also differ in the number of allosauroid terminal taxa. The current study employs nine terminals, whereas Currie & Carpenter (2000) use five (*Acrocanthosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Giganotosaurus*, *Sinraptor*). To examine the effect of differential taxonomic sampling, *Neovenator* was scored for the 110 characters of Currie & Carpenter (2000) and the matrix (without any scoring changes from the original) was rerun using PAUP* (Supplementary Appendix 4). Due to their incompleteness, *Eocarcharia* and *Tyrannotitan* were not included. Two most parsimonious trees of 230 steps resulted, the strict consensus of which places *Neovenator* as the sister taxon to *Acrocanthosaurus* (Figure 9A). The relative positions of the other five taxa do not change. Thus, taxonomic sampling is not a major source of incongruence between the two analyses.

In summary, while taxonomic sampling is not likely an important source of topological incongruence between the current analysis and that of Currie & Carpenter (2000), scoring differences and character choice are critical.

Finally, Coria & Currie (2006) utilize the character list and data matrix of Currie & Carpenter (2000), to which they added *Mapusaurus* and changed 10 scores for *Giganotosaurus*, five for *Allosaurus*, two for Sinraptoridae, and two for *Carcharodontosaurus*. This analysis recovers *Mapusaurus* as the sister taxon to *Giganotosaurus*, and agrees with the earlier analysis of Currie & Carpenter (2000) in all other aspects of allosauroid phylogeny. The current analysis also recovers *Giganotosaurus* and *Mapusaurus* as sister taxa.

Allain 2002

The topology presented here also agrees with that of Allain (2002) only in the sister-group relationship between *Carcharodontosaurus* and *Giganotosaurus*. Allain (2002) finds *Acrocanthosaurus* and *Allosaurus* as sister taxa, and *Sinraptor* as the immediate outgroup to Carcharodontosauridae (a node supported by relatively low bootstrap and Bremer support values of 46% and 1, respectively). In contrast, the current analysis finds *Sinraptor* as the most basal allosauroid and *Acrocanthosaurus* as a carcharodontosaurid.

Four synapomorphies linked *Acrocanthosaurus* and *Allosaurus* in Allain's (2002) study, including the aforementioned problematic characters concerning the basal tubera (character 15), paroccipital processes (32), and external mandibular fenestra (44). These two taxa were also united by a keyhole-shaped infratemporal fenestra (character 41). However, *Carcharodontosaurus* and *Giganotosaurus* were scored for the primitive state, even though the pertinent circumtemporal bones are not known. This character is rendered ambiguous when these taxa are scored correctly.

Two synapomorphies united *Sinraptor* and carcharodontosaurids in Allain's (2002) study: a posteroventrally-sloping occiput (character 43) and a reversal to a non-pneumatized opening for the internal carotid (character 23). While we agree that the first synapomorphy is valid, problems with the second character are discussed above; this character is too variable and poorly defined to accurately score.

Among the 12 characters shared between the two analyses, seven scoring differences exist, two of which involve positive scores (Supplementary Appendix 2). Rerunning Allain's (2002) dataset with the scores favored by the current analysis results

in 52 most parsimonious trees of length 86, compared to three MPTs of length 83 in the original analysis. The strict consensus of these trees (Figure 8B) shows little resolution, with only the *Carcharodontosaurus* + *Giganotosaurus* sister group remaining. *Sinraptor*, *Acrocanthosaurus*, and *Allosaurus* fall into a polytomy with Carcharodontosauridae at the base of Allosauroidea. This suggests that scoring differences are a source of incongruence between our topology and that of Allain (2002).

Allain's (2002) analysis also differs considerably in the number, distribution, and use of informative characters. Allain (2002) includes only cranial characters, 13 of which are informative at the level of Allosauroidea. In the present analysis, 12 of the 99 characters (12%) are also used by Allain (2002). Furthermore, the present analysis includes only eight of the 13 informative characters used by Allain (2002) (62%; Supplementary Appendix 3). Two of these rejected characters are synapomorphies of *Allosaurus* + *Acrocanthosaurus* (characters 23, 32) and are discussed above. One is a synapomorphy of *Carcharodontosaurus* and *Giganotosaurus* (42), one links *Allosaurus* and *Sinraptor* (20), and one unites *Allosaurus*, *Sinraptor*, and *Acrocanthosaurus* (6). Additionally, Allain (2002) does not include several characters, many of which are postcranial, that unite *Acrocanthosaurus* with carcharodontosaurids and place *Sinraptor* as basal in the present study.

Allain (2002) includes only five allosauroid terminal taxa, excluding *Neovenator*, as well as *Eocarcharia*, *Mapusaurus*, and *Tyrannotitan*, which were not known at the time of his analysis. When *Neovenator* was scored for Allain's (2002) 45-character dataset and the matrix rerun in PAUP* (Supplementary Appendix 4), 52 most parsimonious trees of length 84 resulted. The strict consensus recovers little structure, as only the *Carcharodontosaurus* + *Giganotosaurus* sister grouping is recovered and all other allosauroids fall into a polytomy, which also includes several non-allosauroid taxa (Figure 9B). Therefore, taxonomic sampling is also a source of incongruence between the current study and Allain's (2002).

In summary, scoring differences, character choice, and taxonomic sampling may all play a role in the incongruence between our analysis and that of Allain (2002).

Novas *et al*. 2005

The topology of Novas *et al*. (2005) is very similar to that found by Allain (2002), and differs substantially from that recovered here. Like Currie & Carpenter (2000) and Allain (2002), Novas *et al*. (2005) find support for an *Acrocanthosaurus* + *Allosaurus* sister group relationship (but with a low bootstrap support of 41% and Bremer support of 1). Additionally, although the cladogram reported by Novas *et al*. (2005, Figure 3) shows *Sinraptor* as basal to all other allosauroid taxa, reanalysis of their data positions *Sinraptor* as the closest outgroup to Carcharodontosauridae. As the tree statistics are identical in the published and reanalyzed tree, it is assumed that the published tree was mistakenly included.

Novas *et al*. (2005) find 11 synapomorphies linking *Acrocanthosaurus* and *Allosaurus*. Of these, characters concerning accessory antorbital openings (character 1), the trigeminal foramen (19), the external mandibular fenestra (21), scapulocoracoid notch (44), metacarpal 4 (51), basal tubera (78), paroccipital processes (79), and internal carotid artery (80) are discussed as problematic above. Three additional characters are discussed below.

Internal Mandibular Fenestra: Novas *et al*. (2005, character 22) scored *Acrocanthosaurus* and *Allosaurus* as possessing a splenial that is notched to form the anterior margin of the internal antorbital fenestra. *Sinraptor* is scored for the primitive state, and *Carcharodontosaurus*, *Giganotosaurus*, and *Tyrannotitan* are scored "?." However, published figures suggest that the splenial of *Sinraptor* is notched for the internal mandibular fenestra (Currie & Zhao 1993: Fig 11). With this corrected score, all allosauroids with known splenials are scored for the derived state.

Haemal Arch Shape: *Acrocanthosaurus* and *Allosaurus* were scored for L-shaped haemal arches on the distal caudal vertebrae (character 41), whereas *Giganotosaurus* was scored as lacking an L-shape and *Carcharodontosaurus*, *Sinraptor*, and *Tyrannotitan* were scored "?." However, as far as we are aware, no chevrons are known for *Giganotosaurus* beyond the mid caudal vertebrae. Even if the distal chevrons of *Giganotosaurus* are not L-shaped, however, this is best interpreted as a reversal, as several allosauroid outgroups (*Torvosaurus*, compsognathids) possess L-shaped chevrons, which have been interpreted by many authors (e.g., Sereno *et al*. 1996) as diagnostic of Neotetanurae.

Basipterygoid Processes: Novas *et al*. (2005, character 20) scored *Acrocanthosaurus* and *Allosaurus* as possessing long basipterygoid processes, whereas *Sinraptor* was scored for the primitive condition (short processes) and other allosauroids were scored "?." This character has been used in many studies of theropod phylogeny, but rampant scoring disagreement persists. We could not sufficiently quantify this character, so it is rejected in the present analysis.

Sinraptor was united with Carcharodontosauridae based on eight synapomorphies. Three of these (characters 17, 92, 93), dealing with the posteroventrally-sloping occiput, are here considered redundant. However, as discussed above, a posteroventrally-sloping occiput is accepted as a valid synapomorphy of *Sinraptor* and carcharodontosaurids. Additionally, several braincase characters (91, 94), originally identified by Coria & Currie (2002) and included by Novas *et al*. (2005), are also accepted as valid here. Three additional synapomorphies deserve comment.

Postorbital Flange: Novas *et al*. (2005, character nine) scored *Carcharodontosaurus*, *Giganotosaurus*, and *Sinraptor* as possessing a suborbital flange on the postorbital. *Allosaurus* and *Acrocanthosaurus* were scored for the (primitive) lack of this flange, and *Tyrannotitan* was scored "?." However, published figures (Currie & Zhao 1993: Fig 8) and observation of the holotype (IVPP 10600) clearly show that *Sinraptor* does not possess a suborbital flange similar in morphology to the pronounced processes of *Carcharodontosaurus* and *Giganotosaurus*. Rather, *Sinraptor* is characterized by a slight rugosity on the anterior edge of the ventral ramus of the postorbital. Furthermore, personal observation of the holotype (OMNH 10146) reveals that *Acrocanthosaurus* is characterized by such a flange, although it is broken (Figure 7D). Thus, the suborbital flange appears to be a synapomorphy of *Acrocanthosaurus*, *Carcharodontosaurus*, and *Giganotosaurus*, and is optimized as diagnostic of this carcharodontosaurid subgroup in the present analysis.

Axial Intercentrum: *Giganotosaurus* and *Sinraptor* were scored for a dorsally-tilted ventral margin of the axial intercentrum (character 28), whereas *Acrocanthosaurus* and *Allosaurus* were scored for the primitive parallel-trending intercentrum and *Carcharodontosaurus* and *Tyrannotitan* were scored "?." While we agree that *Acrocanthosaurus* (and also *Neovenator*) should be scored for the primitive state, new

material of *Allosaurus* (Chure 2000), along with careful examination of published figures (Madsen 1976: Plate 11), suggests that this taxon should also be scored for the derived state. As a result, this character is now diagnostic of a much more inclusive clade.

Supraoccipital Expansion: Novas *et al*. (2005, character 97) scored *Carcharodontosaurus*, *Giganotosaurus*, and *Sinraptor* for a derived supraoccipital with a dorsal expansion that is at least two times the width of the foramen magnum. *Allosaurus* and *Acrocanthosaurus* were scored for the primitive state, and *Tyrannotitan* scored "?." Measurements of allosauroid braincases, as well as interpretation of published figures (Madsen 1976: Fig 13; Currie & Zhao 1993: Fig 3, 7; Coria & Currie 2002: Fig 5), indicates that no allosauroids possess a supraoccipital expansion more than twice the width of the foramen magnum. Additionally, no significant differences in supraocciptal morphology were found. Thus, this character is discarded in the present analysis.

Finally, Novas *et al*. (2005) list several characters diagnostic of their Carcharodontosauridae, which includes *Carcharodontosaurus*, *Giganotosaurus*, and *Tyrannotitan*, but not *Acrocanthosaurus*. Of these characters, a dentary with a squared-off anterior end (25), postaxial cervicals with two pleurocoels (32), and pleurocoels throughout the dorsal vertebral column (34) are also found in *Acrocanthosaurus*.

Among the 37 characters shared between the current analysis and that of Novas *et al*. (2005), 29 scoring differences exist, 18 involving positive scores (Supplementary Appendix 2). Rerunning the dataset of Novas et al. (2005) with the scores favoured by the present analysis results in one most parsimonious tree of 235 steps (CI=0.55, RI=0.62), compared to one MPT of length 227 in the original analysis. This tree (Figure 8C) is remarkably different from that of the original analysis: *Acrocanthosaurus* and *Allosaurus* are no longer sister taxa and *Giganotosaurus* and *Tyrannotitan* comprise a clade exclusive of *Carcharodontosaurus*. This suggests that scoring differences are a source of incongruence between our topology and that of Novas *et al*. (2005), especially concerning the placement of *Acrocanthosaurus*.

The present analysis and that of Novas *et al*. (2005) also differ in the number and distribution of informative characters. Novas *et al*. (2005) use 48 informative characters, 26 of which are also utilized in the present analysis (54%; Supplementary Appendix 3). Overall, 37 of the 99 characters used in the present analysis also appear in the character

list of Novas *et al*. (2005) (37%). As outlined above, six of these characters are synapomorphies of *Acrocanthosaurus* and *Allosaurus* (20, 22, 36, 41, 79, 80), and three link *Sinraptor* and carcharodontosaurids (17, 92, 97). Additionally, Novas et al. (2005) did not utilize several characters that unite *Acrocanthosaurus* with carcharodontosaurids and place *Sinraptor* as basal in the present study.

The analysis of Novas *et al*. (2005) includes six allosauroid terminal taxa. They introduce *Tyrannotitan* as a new basal carcharodontosaurid but did not include *Neovenator*, another taxon with a potentially similar position among allosauroids. When *Neovenator* is added, their analysis yields a single most parsimonious tree of 230 steps (Figure 9C, Supplementary Appendix 4). *Neovenator* is recovered as the sister taxon to *Acrocanthosaurus*, and the relative positions of the other allosauroid taxa remain unchanged.

In summary, scoring differences and character choice are sources of incongruence between the present analysis and that of Novas *et al*. (2005), but taxonomic sampling likely does not explain topological differences.

Holtz 2000

The analysis of Holtz (2000) agrees with the present study in most aspects, the lone exception being the sister group relationship between *Allosaurus* and *Neovenator*. Holtz (2000) presents three unambiguous synapomorphies supporting this grouping: five premaxillary teeth (character 3), moderately elongated distal caudal prezygapophyses that extend more than one half but less than one times the length of the centrum (character 199), and a reversal to a broad distal scapula expansion (character 212). We agree that five premaxillary teeth uniquely characterize these two taxa. However, new illustrations of *Neovenator* (Hutt 1999) and reexamination of the holotype (MIWG 6348/BMNH R1001) clearly show elongated distal caudal prezygapophyses. Furthermore, measurement of allosauroid scapulae reveals no quantifiable pattern in distal scapular expansion width.

DISCUSSION AND IMPLICATIONS

Current consensus in allosauroid phylogeny

Allosauroids have been the subject of many phylogenetic analyses. Consensus, however, has been slow to emerge, as cladistic analyses continue to disagree on the position of *Sinraptor*, *Acrocanthosaurus*, and *Neovenator*. The only consistent node among various studies has been the grouping of derived carcharodontosaurids (*Carcharodontosaurus* and *Giganotosaurus*), which is found in nearly every published analysis. The discovery of new taxa (Hutt *et al*. 1996, Novas *et al*. 2005, Coria & Currie 2006, Sereno & Brusatte in press) and the publication of three detailed theropod phylogenies (Holtz 2000, Rauhut 2003, Holtz *et al*. 2004) have done little to resolve problematic areas of allosauroid phylogeny. Frustratingly, despite an average publication rate of over one new allosauroid phylogenetic study per year, only cursory discussion has been devoted to similarities and differences among analyses. As a result, problematic characters have endured in the literature and coding differences have proliferated.

Based on the new analysis and comparisons with previously-published studies, the current state of allosauroid phylogeny can be assessed. The analysis presented here, which consists of 99 characters scored across nine ingroup taxa, integrates previously-published characters with several new characters. Some published characters were rejected, but reasons for these have been noted (Supplementary Appendix 3). Additionally, the new analysis also includes several newly-described taxa (*Eocarcharia*, *Mapusaurus*, *Tyrannotitan*) and data from newly-available material.

The recovered most parsimonious cladogram (Figure 5) plaes *Sinraptor* as a basal allosauroid, a position supported by robust Bremer support (5) and boostrap (84%) measures for the less inclusive *Allosaurus* + Carcharodontosauridae node. This conflicts with several previous studies that place *Sinraptor* as the sister taxon to Carcharodontosauridae. In two such analyses (Allain 2002, Novas *et al*. 2005), several braincase characters provided key support for uniting these two taxa. Although most of these characters are included in the present analysis, many other characters from other skeletal regions unite *Allosaurus* and Carcharodontosauridae to the exclusion of *Sinraptor* (19 characters under ACCTRAN, 20 under DELTRAN, 14 unambiguous). Many of these characters are not included in the analyses of Allain (2002) and Novas *et al*. (2005). Two non-braincase characters linking *Sinraptor* and carcharodontosaurids in

the latter study are rejected here because of what we regard as errors in character state scores. Due to this character support, as well as the high tree support measures discussed above and problems with characters from other analyses, the basal position of *Sinraptor* appears to be well supported by the present dataset.

The present analysis places *Acrocanthosaurus* within Carcharodontosauridae, a position robustly supported by numerous characters and relatively high Bremer support and bootstrap values (Figure 5). An additional 27 steps are required to reposition *Acrocanthosaurus* as the sister taxon to *Allosaurus*, as is advocated by many alternative studies. Five characters in the current study do unite *Acrocanthosaurus* and *Allosaurus* (30, 48, 55, 56, 58), but these are ambiguous due to missing data in carcharodontosaurids. Although the analyses of Currie & Carpenter (2000), Allain (2002), and Novas *et al*. (2005) each unite *Acrocanthosaurus* and *Allosaurus*, nearly every supporting synapomorphy appears problematic, and bootstrap and Bremer support values supporting this grouping are weak (Figure 2). Furthermore, when incongruent scores are changed to those favoured in the present analysis, the *Acrocanthosaurus* + *Allosaurus* grouping found in all three alternative studies collapses. Thus, the carcharodontosaurid affinity of *Acrocanthosaurus* is considered strongly supported by the present analysis, whereas an *Acrocanthosaurus* + *Allosaurus* sister relationship is highly unparsimonious and supported by few data.

The interrelationships within Carcharodontosauridae are less secure, as several taxa are based on fragmentary material. The position of *Neovenator* as closer to *Carcharodontosaurus* than to *Allosaurus* is considered robust, however, due to several synapomorphies (29 under ACCTRAN, 11 under DELTRAN, 10 unambiguous) and high tree support values (Bremer support=5, bootstrap=90%). Although Holtz (2000) recovered *Neovenator* and *Allosaurus* as sister taxa, our review of the character evidence leaves only one supporting character. The sister group relationship between *Carcharodontosaurus* and the *Giganotosaurus* + *Mapusaurus* clade also appears to be robust, as it is supported here by high tree support values (Bremer support=2, bootstrap=91%) and numerous synapomorphies (18 under ACCTRAN, 16 under DELTRAN, 13 unambiguous), and has been recovered in most previous analyses. Future work may find support for a clade of endemic South American carcharodontosaurids,

with the poorly-known *Tyrannotitan* repositioned closer to *Giganotosaurus* than to *Carcharodontosaurus* and more basal carcharodontosaurids. This is currently less parsimonious with the present dataset, but abundant missing data in *Tyrannotitan* renders its placement somewhat problematic. Indeed, when conflicting scores in the analysis of Novas *et al*. (2005) are changed to those favoured by the current analysis *Tyrannotitan* moves from a basal carcharodontosaurid position to a sister-group seem secure.

Finally, the number of previously published characters rejected in the current analysis may appear alarming (Supplementary Appendix 3). However, each of the 12 published analyses considers allosauroids along with several non-allosauroid taxa, and many employ vastly different outgroups. Although some characters are found to be informative in the original analyses, comparison with allosauroid outgroups often reveals extreme variation, rendering polarity determination difficult and suggesting that the character may have little phylogenetic utility. Furthermore, in our experience large-scale theropod phylogenetic analyses are especially prone to incorrect scores and redundant characters (for example, scores for characters 555-578 for *Carcharodontosaurus* seem to be accidentally shifted one space in the analysis of Holtz *et al*. 2004), which may artificially inflate the number of characters informative at a single node, such as Allosauroidea. Regardless, every character informative at the level of Allosauroidea in each of the 12 analyses was carefully considered for this study.

Character evolution in Allosauroidea

Several characters of particular note are discussed below. A complete list of synapomorphies for each allosauroid clade is provided in Supplementary Appendix 1.

Carcharodontosaurus and *Giganotosaurus* are united by several synapomorphies, most of which are cranial. Many of these synapomorphies involve bone texture, fusion, and the highly apomorphic morphology of the braincase. Carcharodontosauridae, by contrast, is diagnosed by both cranial and postcranial synapomorphies. More exclusive clades within Carcharodontosauridae are united by characters related to vertebral pneumatism, which is prone to individual (Chure & Madsen 1996) and ontogenetic (Rauhut & Fechner 2005) variation. While this may be problematic, copious additional synapomorphies also unite clades within Carcharodontosauridae. Furthermore, although

Currie & Carpenter (2000) dismiss several synapomorphies of *Acrocanthosaurus* and Carcharodontosaurinae as size-related, many of these are seen in the much smaller *Eocarcharia* (Sereno & Brusatte in press), and are not seen in other large-bodied theropods such as spinosaurids. Although Currie & Carpenter (2000) are correct in asserting that *Acrocanthosaurus* lacks many derived characters seen in *Carcharodontosaurus* and *Giganotosaurus*, including heavily-sculptured cranial bones and the highly-derived braincase, these characters are here interpreted as synapomorphies of the derived Carcharodontosaurinae. Their absence in *Acrocanthosaurus* does not contradict its placement as closer to *Carcharodontosaurus* than to *Allosaurus*.

The phylogenetic analysis presented here is highly homoplastic, and consequently many putative synapomorphies are rejected as nonhomologous among taxa. Foremost among these are the many braincase characters that unite *Sinraptor*, *Carcharodontosaurus*, and *Giganotosaurus* to the exclusion of *Acrocanthosaurus* and *Allosaurus*. Based on the recovered topology, it is most parsimonious to conclude that these characters evolved independently in *Sinraptor* and Carcharodontosaurinae. Similarly, five premaxillary teeth may have alternatively evolved in the common ancestor of *Allosaurus* and Carcharodontosauridae and been lost in all carcharodontosaurids more derived than *Neovenator*, or they may have arisen independently in *Allosaurus* and *Neovenator*.

Status of controversial taxa

Several theropod taxa not included in this analysis have been recovered as allosauroids in previous higher-level analyses of theropod phylogeny. The current study cannot adequately test the phylogenetic relationships of these taxa, as this would require the inclusion of a diverse array of non-allosauroid terminal taxa. However, some of these taxa are briefly discussed below, along with character support for their inclusion in Allosauroidea.

Abelisauridae. Some authors (Novas 1997, Sampson *et al*. 1998) have noted numerous similarities between carcharodontosaurids and the Cretaceous abelisaurid theropods. Although most studies place abelisaurids as basal theropods closely related to

Ceratosaurus, Forster (1999) positioned abelisaurids among basal tetanurans, and thus more closely related to allosauroids than to other primitive theropods. Carcharodontosaurids share with abelisaurids several cranial similarities, including a postorbital-lacrimal contact excluding the frontal from the orbital rim, a suborbital flange on the postorbital, an anteroventrally-oriented ventral process of the postorbital, fused frontal-parietal sutures, and heavily textured cranial bones. However, abelisaurids lack many other tetanuran and allosauroid synapomorphies, and character states in basal members of both clades (*Rugops*: Sereno *et al*. 2004; *Eocarcharia*: Sereno & Brusatte in press) suggest that most of the features shared between carcharodontosaurids and abelisaurids evolved independently. Thus, an allosauroid (or tetanuran) placement for abelisaurids is highly unparsimonious, and the similarities between these two clades are best interpreted as convergences.

Monolophosaurus. Some analyses (e.g., Sereno *et al*. 1996, Holtz 2000, Currie & Carpenter 2000, Novas *et al*. 2005) have positioned the Chinese *Monolophosaurus* nested within the stem-based Allosauroidea, whereas others have placed it in an unresolved polytomy with many disparate taxa (Harris 1998, Rauhut 2003). *Monolophosaurus* shares with *Allosaurus* and *Neovenator* a square-shaped premaxillary body and a maxilla with a vertical articulation for the premaxilla. These characters, however, appear to have a broader distribution among basal tetanurans. Like all scorable allosauroids other than *Sinraptor*, the infratemporal fenestra of *Monolophosaurus* is constricted by an inflection from the squamosal. Additionally, *Monolophosaurus* possesses a highly pneumatic jugal, rugose nasals, and nasals and lacrimals with raised crests like many allosauroids. However, these latter features are difficult to compare topologically and thus homologize with allosauroids due to the highly autapomorphic cranial crest of *Monolophosaurus*. Although *Monolophosaurus* is positioned as more derived than *Sinraptor* when included in the present analysis, many aspects of its morphology suggest that its affinities lie elsewhere (Brusatte *et al*. in prep).

Cryolophosaurus. Sereno *et al*. (1996) recovered the Early Jurassic Antarctic genus *Cryolophosaurus* as an allosauroid based on an examination of the skull. Most other

analyses have not included this highly incomplete taxon. A recent analysis based on the complete skeleton, discussed only in an abstract (Smith *et al*. 2005), placed *Cryolophosaurus* as a basal tetanuran. As this taxon is currently under study by N. D. Smith *et al*., it will not be discussed here.

Siamotyrannus. Originally described as a basal tyrannosauroid (Buffetaut *et al*. 1996), *Siamotyrannus* was recovered as an allosauroid by Rauhut (2003) and Holtz *et al*. (2004). *Siamotyrannus* possesses an expanded anterior projection of the pubic boot like many allosauroids except *Sinraptor*. Furthermore, the ischia of *Acrocanthosaurus* and *Siamotyrannus* are marked by a distinct muscle attachment scar on the posterior surface. Thus, *Siamotyrannus* may be a carcharodontosaurid, but a careful reexamination of the fragmentary type material is needed before the phylogenetic relationships of this taxon can be critically assessed.

Lourinhanosaurus. Described as an allosauroid by Mateus (1998), *Lourinhanosaurus* has only been included in one cladistic analysis (Holtz *et al*. 2004), which corroborates this placement. Like *Allosaurus*, *Sinraptor*, and *Siamotyrannus*, *Lourinhanosaurus* is characterized by an ilium with a straight anterior margin (character 77). However, recently it has been suggested that this taxon may be a spinosauroid (Allain 2005).

Megaraptor. The bizarre but fragmentary Late Cretaceous *Megaraptor* was described by Novas (1998) as a large dromaeosaurid, largely due to its sickle-like second pedal ungual. The discovery of additional specimens (Lamanna *et al*. 2004, Calvo *et al*. 2004) revealed this claw to be a manual element, thus erasing any significant support for dromaeosaurid affinities. Calvo *et al*. (2004) noted that *Megaraptor* resembled carcharodontosaurids in several vertebral features, and Lamanna *et al*. (2004) briefly discussed a cladistic analysis that recovered this taxon as the basalmost allosauroid, but a list of characters and codings was not presented. In the present analysis, *Megaraptor* shares with many carcharodontosaurids caudal pleurocoels and a strongly hooked coracoid. However, as with *Monolophosasurus*, the phylogenetic relationships of *Megaraptor* can only be tested within the context of a larger analysis of basal tetanurans.

Fukuiraptor. This large theropod from the Albian of Japan has been included in the cladistic analyses of Azuma & Currie (2000) and Holtz *et al*. (2004), which recovers it as an allosauroid. In the present character list, *Fukuiraptor* shares with all scorable allosauroids other than *Sinraptor* a pronounced medial epicondyle of the femur (character 85) and a strongly hooked posteroventral process of the coracoid (character 95). Like *Monolophosaurus*, *Fukuiraptor* is recovered as more derived than *Sinraptor* when included in the present analysis, but must be analyzed by a larger study before its relationships can be confidently assessed.

Phylogenetic taxonomy

Defining clades by reference to tree topology rather than lists of characters or included taxa has become commonplace among archosaur systematists (de Queiroz & Gauthier 1990, 1992; Sereno 1998). Although allosauroid phylogenetic taxonomy has generated much less debate and controversy than that of other theropod clades, alternative definitions exist for all allosauroid taxa. With the help of the new database *TaxonSearch* (Sereno *et al*. 2005), we briefly review the history of allosauroid phylogenetic taxonomy, and propose a revised set of definitions for all taxa. This proposed taxonomy aims to provide stability of membership and preserve priority of definition and original intent where possible. A more complete discussion of allosauroid taxonomy and a list of all proposed definitions can be found in the *TaxonSearch* file "Stem Archosauria" (Sereno 2005; Sereno *et al*. 2005; www.taxonsearch.org). An abbreviated version of our preferred definitions is provided in Table 2, and names are applied to clades in Figure 5.

Allosauroidea. This superfamily-level taxon, attributed to Marsh (1878) who coined Allosauridae, was first explicitely utilized by Currie & Zhao (1993). They included the family-level Allosauridae and Sinraptoridae and excluded other basal tetanurans, such as "megalosaurs" and *Monolophosaurus*. Padian & Hutchinson (1997) provided the first definition of Allosauroidea: *Allosaurus* and *Sinraptor* and all descendants of their most recent common ancestor. Independently, Sereno (1998) defined Allosauroidea as a stem-

based clade encompassing all neotetanurans closer to *Allosaurus* than to Neornithes. A similar stem-based definition, however, was coined for the clade Carnosauria (Padian & Hutchinson 1997; Padian *et al*. 1999; Holtz *et al*. 2004). These node and stem-based definitions may differ in content, as some basal tetanurans that fall outside the *Sinraptor* + *Allosaurus* node would be considered allosauroids in the taxonomy of Sereno (1998, 2005), but non-allosauroid carnosaurs in the system of Padian and others. While basal tetanuran phylogeny is still unresolved, some analyses (Holtz 2000, Rauhut 2003, Holtz *et al*. 2004) suggest that taxa such as *Monolophosaurus* and *Fukuiraptor* may occupy this problematic zone. We advise against the continued use of Carnosauria, due to its long history as a "wastebasket" taxon for a phylogenetically disparate array of large theropods (tyrannosaurids, abelisaurids, allosaurids). Given the current state of flux of basal tetanuran phylogeny, we favor a stem-based definition for Allosauroidea that may eventually absorb several poorly-known taxa, if new information suggests they lie closer to *Allosaurus* than to birds. Thus, the preferred definition of Allosauroidea is: **the most inclusive clade containing *Allosaurus fragilis* Marsh 1877, but not *Passer domesticus* Linnaeus 1758.**

In the future, as the relationships of *Monolophosaurus*, *Fukuiraptor*, *Lourinhanosaurus*, and spinosauroids become clearer, it may be useful to name a node-based taxon to encompass Allosauridae and Carcharodontosauridae (and likely Sinraptoridae) to the exclusion of more basal allosauroids. This node would be equivalent to Allosauroidea as defined by Padian & Hutchinson (1997), Padian *et al*. (1999), and Holtz *et al*. (2004), and essentially encompasses the nine ingroup taxa in the current analysis. However, until the relationships of basal tetanurans and basal allosauroids are better resolved, we choose not to name such a node here.

Allosauridae. Coined by Marsh (1878), Allosauridae was originally defined as a stem-based clade encompassing theropods closer to *Allosaurus* than to *Sinraptor* (Padian & Hutchinson 1997). Independently, Sereno (1998) used a similar definition but added *Carcharodontosaurus*, *Monolophosaurus*, *Cryolophosaurus*, and eventually the neornithine *Passer* (Sereno 2005) as external specifiers to better limit potential included taxa in the event that Allosauroidea is not monophyletic. Sereno's (2005) definition is

followed here: **the most inclusive clade containing *Allosaurus fragilis* Marsh 1877, but not *Sinraptor dongi* Currie and Zhao 1993, *Carcharodontosaurus saharicus* Depéret and Savornin 1927, or *Passer domesticus* Linnaeus 1758.**

Sinraptoridae. This clade name was first used by Currie & Zhao (1993), first defined by Padian & Hutchinson (1997) as a stem-based taxon, and revised by Sereno (1998, 2005), who added several external specifiers. Sereno's (2005) definition is followed here: **the most inclusive clade containing *Sinraptor dongi* Currie and Zhao 1993, but not *Allosaurus fragilis* Marsh 1877, *Carcharodontosaurus saharicus* Depéret and Savornin 1927, or *Passer domesticus* Linnaeus 1758.**

Carcharodontosauridae. Coined by Stromer (1931) and first defined by Sereno (1998) as a stem-based taxon, we follow Sereno's (2005) revised definition here: **the most inclusive clade containing *Carcharodontosaurus saharicus* Depéret and Savornin 1927, but not *Sinraptor dongi* Currie and Zhao 1993, *Allosaurus fragilis* Marsh 1877, or *Passer domesticus* Linnaeus 1758.**

Carcharodontosaurinae. The discovery of new genera (*Eocarcharia*, *Tyrannotitan*) and the corroboration of the carcharodontosaurid affinities of *Neovenator* have greatly expanded the membership of Carcharodontosauridae. Ingroup relationships within the clade are problematic due to high amounts of missing data, but the close relationship between *Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus* is highly supported by robust tree support measures, enumerated by several synapomorphies, and corroborated by nearly every published cladistic analysis. As increased fossil collecting in Africa and South America make it probable that close relatives of these genera will be discovered, we elect to use Carcharodontosaurinae to refer to the highly derived, large-bodied carcharodontosaurids. This clade is here defined as: **the least inclusive clade containing *Carcharodontosaurus saharicus* Depéret and Savornin 1927 and *Giganotosaurus carolinii* Coria and Salgado 1995.**

Giganotosaurini. In their description of *Mapusaurus*, Coria & Currie (2006) named the new taxon Giganotosaurinae to refer to those carcharodontosaurids closer to *Giganotosaurus* and *Mapusaurus* than to *Carcharodontosaurus*. We feel, however, that the subfamily-level taxon Carcharodontosaurinae, which has long been available as a coordinate taxon of Carcharodontosauridae Stomer 1931, is most useful and appropriate to encompass the clade of highly-derived, large-bodied carcharodontosaurids including *Carcharodontosaurus*. Giganotosaurinae would then be included within another taxon (Carcharodontosaurinae) with an identical Linnean suffix. To preserve the traditional hierarchy of Linnaean suffixes, we therefore erect Giganotosaurini to replace Giganotosaurinae, as defined by Coria & Currie (2006). Giganotosaurini is here defined as: **the most inclusive clade containing *Giganotosaurus carolinii* Coria and Salgado 1995, but not *Carcharodontosaurus saharicus* Depéret and Savornin 1927**. In this way, Giganotosaurini includes carcharodontosaurines most closely related to *Giganotosaurus* among carcharodontosaurids. In this classification scheme, it would be possible to erect a subfamily-level taxon for those taxa close to *Acrocanthosaurus* and a tribe-level taxon for those taxa more closely related to *Carcharodontosaurus* than to *Giganotosaurus*, should the requisite specimens be discovered.

Stratigraphic congruence

Cladistic hypotheses imply a relative temporal ordering of branching events in a clade's history (Figure 10). Ideally, since there is one true history of life, this hierarchically-arranged ordering should be congruent with the linear stratigraphic succession of the clade's fossil record. In recent years, workers have devised several metrics to quantify the congruence between a specific phylogenetic hypothesis and the known fossil record of the clade in question. These metrics fall into two categories: gap metrics, which measure sampling gaps inferred by a specific phylogenetic hypothesis (RCI: Benton & Storrs 1994; GER: Wills 1999; MSM*: Siddall 1998, Pol & Norell, 2001; RI_S: Fisher 1992, Clyde & Fisher 1997, Finarelli & Clyde 2002), and consistency metrics, which compare the rank order of cladistic branching with the first appearance of terminal taxa in the fossil record (SRC: Gauthier *et al*. 1988, Norell & Novacek 1992; SCI: Huelsenbeck 1994; see review in Wagner & Sidor [2000]). Although these metrics are

all designed to measure the fit of stratigraphy to a cladogram, considerable debate persists over the potential biases and relevant uses of each. In particular, simulation studies have clearly shown that these metrics are often sensitive to tree size, tree shape, sampling intensity, and the stratigraphic ages of terminal taxa (Norell & Novacek 1992; Siddall 1996, 1997; Hitchin & Benton 1997; Wills 1999; Pol & Norell 2001; Pol *et al*. 2004).

Although potential problems exist with every stratigraphic metric yet devised, some metrics are more robust than others (Pol *et al*. 2004), and can be useful for measuring both the stratigraphic fit of a specific phylogenetic hypothesis, as well as the relative stratigraphic fits of alternative hypotheses for the same clade. In these cases, knowledge of stratigraphic congruence can build or weaken confidence in a specific hypothesis, and help choose between competing hypotheses, repectively. This is especially true for allosauroids, a clade described by several competing phylogenetic hypotheses. Along with the character data discussed above, the relative stratigraphic fits of alternative hypotheses can be used as a measure of comparison. Choosing which metric(s) to use is difficult, but three in particular are well-suited for an extinct group of terrestrial vertebrates known almost entirely from "point occurrences" in the fossil record. These metrics include the Stratigraphic Consistency Index (SCI: Huelsenbeck 1994), the Gap Excess Ratio (GER: Wills 1999), and the modified Manhattan Stratigraphic Measure (*MSM: Siddall 1998, Pol & Norell 2001). Complete definitions of each of these metrics can be found in the literature, as well as discussion of potential biases (see Pol *et al*. 2004 for an overview).

A list of these metrics compiled for the current study and several alternative hypotheses is presented in Table 5. For all comparisons, the current study is pruned to a common set of taxa (five shared taxa for comparisons with the analyses of Allain 2002, Coria & Currie 2002, and Novas *et al*. 2005, and six shared taxa for comparisons with Holtz 2000), thus eliminating all potential biases except for those relating to tree shape.

With its full set of nine allosauroid terminal taxa, the present analysis is characterized by high values for all three metrics. For the MSM*, the current analysis is stratigraphally congruent at the p=0.002 level—that is, less than 0.2% of the time would a stratigraphic fit that is better than the observed fit be expected. Thus, the current analysis is considered to be largely congruent with stratigraphy. Although the Spearman Rank

Correlation, which plots clade rank against age rank (Gauthier *et al*. 1988), has fallen widely out of use due to its biases, this metric is well-suited to the largely pectinate topology found by the current analysis. Plotting clade rank vs. age rank (based on earliest known occurrence) for individual clades, with the *Acrocanthosaurus* + *Eocarcharia* node collapsed following Norell & Novacek (1992), gives an SRC of 0.91. This correlation is significant at the $p<0.0009$ level, and in fact all deviation from a perfect SRC (SRC=1.0) is due solely to the statistical problem of identical ages for several terminal taxa. This indicates that the known fossil record, coupled with the present phylogeny, is a good representation of allosauroid history.

When pruned to a common set of taxa and compared to several alternative phylogenies, the current analysis is consistently more congruent with stratigraphy than any competing published analysis. The large discrepancy between the current analysis and the alternatives is readily shown by the MSM*, which simulations have show is least sensitive to tree size and shape biases among the metrics used here (Pol *et al*. 2004). While the MSM* of the present analysis is significant at the $p=0.05$ level, that of the analyses of Allain (2002), Coria & Currie (2002), and Novas *et al*. (2005), which find *Acrocanthosaurus* and *Allosaurus* as sister taxa and *Sinraptor* as the sister taxon to the Carcharodontosauridae, are only significant at the $p=0.80$ level. In other words, a better than observed stratigraphic fit would be expected nearly 80% of the time. A second alternative, one which places *Sinraptor* as the most basal allosauroid but maintains an *Acrocanthosaurus* + *Allosaurus* clade, is significant at the $p=0.43$ level. The topology of Holtz (2000), which places *Allosaurus* and *Neovenator* as sister taxa, is significant at the $p=0.05$ level, but has a lower MSM* and much higher p value than the present study. Therefore, when most potential biases are controlled for and a range of stratigraphic congruence metrics are examined, the present study without fail fits stratigraphy more closely than any published alternative.

Finally, allosauroid phylogeny can be examined with stratocladistics, a method that incorporates both morphological and stratigraphic information to generate a hypothesis that minimizes both morphological homoplasy and nonpreservation of lineages (Fisher 1992, Fisher & Clyde 1997, Fox *et al*. 1999, Bodenbender & Fisher 2001). Stratocladistics has been criticized from many angles (Adrain & Westrop 2001,

Sumrall & Brochu 2003), and has only been applied to one published dinosaur dataset, an analysis of sauropod phylogeny (Wilson 2005). Although we have serious philosophical and practical reservations concerning stratocladistics, we believe that it can be valuable as a heuristic tool to identify robust and problematic areas of a phylogenetic reconstruction (Angielczyk & Fox 2006). For this analysis of allosauroids, we used MacClade to score a stratigraphic character, which was conservatively divided into five states that minimize gaps and imprecision in fossil dating (Appendix 2). When added to the current analysis and several alternative datasets, in no case did this stratigraphic character alter the most parsimonious topology. However, the retention index of this character (RI_S), as well as the number of implied interval crossings by nonpreserved lineages (stratigraphic debt: SD), differs for each of the alternative analyses (Table 5). As with the congruence metrics discussed above, the present phylogeny consistently is charactered by a higher RI_S and less stratigraphic debt than any published alternative.

Palaeobiogeography

Allosauroids have figured prominently in discussions of Mesozoic palaeobiogeography because they comprise a long-lived and diverse group which originated when Pangaea was largely coherent and evolved during its fragmentation (Harris 1998; Perez-Moreno *et al*. 1999; Sereno 1999a,b; Upchurch *et al*. 2002). These studies can be divided into two general approaches. The first, or traditional approach, is to combine palaeogeographic data with knowledge of the age, distribution, and relationships of the taxa under study (as well as other co-existing taxa). The finished hypothesis is what might be viewed as a "most probable scenario" (Sereno 1997). For allosauroids, these scenarios have identified a subclade of southern allosauroids, the derived carcharodontosaurids *Carcharodontosaurus* and *Giganotosaurus*, that may well have radiated largely after the isolation of Gondwana during the Cretaceous (Sereno *et al*. 1996; Harris 1998; Perez-Moreno *et al*. 1999; Sereno 1999b).

The second approach is quantitative and attempts to determine palaeogeographic signal independently from phylogenetic relationships. The results of the biogeographic analysis are then compared with palaeogeographic information. These analyses can involve parsimony analysis of endemicity (e.g., Le Loeuff 1991), a method now largely

abandoned, or a variety of manipulations involving area cladograms based on taxon cladograms such as component analysis (Platnick & Nelson 1981), Brooks Parsimony Analysis (Brooks & McLennan 1991, Brooks *et al*. 2001), and three-area statements (Nelson & Ladiges 1991). These methods, which are usually applied to extant taxa with better-resolved distributions, permit one or two important assumptions (Brooks and McLennan 2002). "Assumption 1" allows the insertion of missing lineages to account for conflict that otherwise might require dispersal. Although this method has been applied to dinosaur distribution in general (Upchurch *et al.* 2002), it has not been applied to a theropod clade in particular.

We used one of these methods, three-area analysis (Nelson & Ladiges 1991), to analyze allosauroid biogeography. This method was selected because it is straightforward to implement, can be applied to a single clade, and emphasizes information from cladogram topology—the primary phylogenetic pattern—while minimizing problems due to widespread taxa. A matrix of three-area statements was generated based on our most parsimonious cladogram (Supplementary Appendix 5). When analyzed in PAUP*, this matrix produces a single most parsimonious area tree (TL=30, CI=0.90, RI=0.89; Figure 11), which places North America, Europe, and Asia as successive outgroups to a sister-grouping of Africa and South America. Two nodes show strong bootstrap (1000 replicates) and Bremer support values (Figure 11).

Notably, the topology recovered by three-area analysis matches the most common version of the breakup sequence of Pangaea (Rabinowitz & LaBrecque 1979, Smith *et al*. 1994, Scotese 2004), in which Asia becomes isolated first, followed successively by North America, and then by South America plus Africa. The position of Europe during the breakup is often viewed as equivocal, as much of the European landmass was intermittently exposed as a series of islands during much of the Jurassic and Cretaceous (Smith *et al*. 1994). Congruence between allosauroid phylogeny and Pangaea fragmentation has been noted by previous authors, but based on smaller phylogenetic datasets and a literal reading of phylogeny (the 'first approach' reviewed above: Harris 1998; Sereno 1999a,b). It is significant that a more rigorous cladistic biogeographic method applied to a larger cladistic dataset recovered the same pattern in this analysis.

Taken at face value, the congruence between the area cladogram and the breakup sequence of Pangaea suggest that the fragmentation of this supercontinent was a major driver of allosauroid evolution. However, this seemingly congruent pattern must be tempered by acknowledging that the basal areas on the cladogram are occupied by the oldest (and lone) Jurassic taxa in the analysis. The basal position of northern areas may well be an artifact of sampling the oldest and most primitive taxa. Whereas it is clear that there was an array of Jurassic tetanurans of some kind on southern continents as early as the Middle Jurassic, these remain poorly documented (e.g., Maganuco *et al*. 2007). Additionally, it is surprising that the basal theropods *Ceratosaurus*, *Torvosaurus*, and *Allosaurus*—long known only from western North America—have all been discovered in recent years in coeval Late Jurassic deposits in Portugal (Mateus *et al*. 2006). And finally, we note that the isolation of Africa as part of a larger Gondwanan landmass for much of the Cretaceous remains a hypothesis challenged by many taxa that suggest at least intermittent connection to Europe (Gheerbant & Rage 2006). Thus, more complete fossil sampling and larger phylogenetic analyses that take into account a broader array of potential allosauroids and other basal tetanurans are needed to more confidently assess the hypothesis that allosauroid phylogeny is congruent with and possibly driven by the fragmentation of Pangaea.

CONCLUSIONS

A new analysis of allosauroid theropods based on 99 characters scored across nine ingroup taxa (Figure 5) yielded results that include the following: (1) *Sinraptor* is positioned as the most basal allosauroid of the taxa considered, followed successively by *Allosaurus* and Carcharodontosauridae; (2) *Neovenator* is recovered as a basal carcharodontosaurid rather than as a sister taxon to *Allosaurus*; (3) *Acrocanthosaurus* is strongly supported as a carcharodontosaurid closer to the Gondwanan genera *Carcharodontosaurus* and *Giganotosaurus* than to *Allosaurus*; (4) alternative topologies in the literature are based on important differences in taxonomic sampling, included characters, and scoring differences among shared characters; (5) the topology recovered by the current analysis shows a strong overall match with the stratigraphic record and is

much more congruent with stratigraphy than any alternative study; (6) the biogeographic history of allosauroids is congruent with the breakup sequence of Pangaea, but requires further testing to more confidently assess. Resolution of conflict among competing phylogenetic analyses will only come with increased attention and comparison at the level of character data and specimens. It is hoped that future studies of archosaur phylogeny pay close attention to specific differences with alternative studies, in order to gain a more complete understanding of why cladistic hypotheses continue to disagree even after years of study.

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REFERENCES

Adrain, J. M. & Westrop, S. R. 2001. Stratigraphy, phylogeny, and species sampling in time and space. Pp. 291-322 in J.M. Adrain, G.D. Edgecombe & B.S Lieberman (eds), *Fossils, Phylogeny, and Form: An Analytical Approach*. Kluwer Academic Press, New York.

Alcober, O., Sereno, P. C., Larsson, H. C. E., Martinez, R. & Varricchio, D. 1998. A Late Cretaceous carcharodontosaurid (Theropoda: Allosauroidea) from Argentina. *Journal of Vertebrate Paleontology*, **15**: 16A.

Allain, R. 2002. Discovery of megalosaur (Dinosauria, Theropoda) in the Middle Bathonian of Normandy (France) and its implications for the phylogeny of basal Tetanurae. *Journal of Vertebrate Paleontology*, **22**: 548-563.

_____. 2005. The postcranial anatomy of the megalosaur *Dubreuillosaurus valesdunensis* (Dinosauria Theropoda) from the Middle Jurassic of Normandy, France. *Journal of Vertebrate Paleontology*, **25**: 850-858.

Angielczyk, K. D. & Fox, D. L. 2006. Exploring new uses for measures of fit of phylogenetic hypotheses to the fossil record. *Paleobiology*, **32**: 147-165.

Azuma, Y. & Currie, P. J. 2000. A new carnosaur (Dinosauria: Theropoda) from the Lower Cretaceous of Japan. *Canadian Journal of Earth Sciences*, **37**: 1735-1753.

Bakker, R. T., Williams, M. & Currie, P. J. 1998. *Nanotyrannus*, a new genus of pygmy tyrannosaur, from the latest Cretaceous of Montana. *Hunteria*, **1**: 1-30.

Benton, M. J. & Storrs, G. W. 1994. Testing the quality of the fossil record: paleontological knowledge is improving. *Geology*, **22**: 111-114.

Bininda-Edmonds, O. R. P., Bryant, H. N. & Russell, A. P. 1998. Supraspecific taxa as terminals in cladistic analysis: implicit assumptions of monophyly and a comparison of methods. *Biological Journal of the Linnean Society*, **64**: 101-133.

Bodenbender, B. E. & Fisher, D. C. 2001. Stratocladistic analysis of blastoic phylogeny. *Journal of Paleontology*, **75**: 351-369.

Bristowe, A. & Raath, M. A. 2004. A juvenile coelophysoid skull from the Early Jurassic of Zimbabwe, and the synonymy of *Coelophysis* and *Syntarsus*. *Palaeontologica Africana*, **40**: 31-41.

Britt, B. B. 1991. Theropods of Dry Mesa Quarry (Morrison Formation, Late Jurassic),

Colorado, with emphasis on the osteology of *Torvosaurus tanneri*. *Brigham Young University, Geology Studies*, **37**: 1-72.

Brooks, D. R. & McLennan, D. A. 1991. *Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology*. University of Chicago Press, Chicago.

_____ **&** _____. *The Nature of Diversity*. University of Chicago Press, Chicago.

_____, van Veller, M. G. P. & McLennan, D. A. 2001. How to do BPA, really. *Journal of Biogeography*, **28** :345-358.

Brusatte, S. & Sereno, P. 2005. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and its implications for allosauroid phylogeny. *Journal of Vertebrate Paleontology*, **25(**3): 40A.

_____, & _____. 2006. Basal abelisaurid and carcharodontosaurid theropods from the Elrhaz Formation (Aptian-Albian) of Niger. *Journal of Vertebrate Paleontology*, **26**(3): 46A.

_____, & _____. In press. A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology*.

Buffetaut, E., Suteethorn, V. & Tong, H. 1996. The earliest known tyrannosaur from the Lower Cretaceous of Thailand. *Nature*, **381**: 689-691.

Bybee, P. J., Lee, A. H. & Lamm, E.-T. 2006. Sizing the Jurassic theropod dinosaur *Allosaurus*: assessing growth strategy and evolution of ontogenetic scaling of limbs. *Journal of Morphology*, **267**: 347-359.

Calvo, J. O. 1999. Dinosaurs and other vertebrates of the Lake Ezequiel Ramos Mexia area, Neuquen-Patagonia, Argeintia. Pp. 13-45 in Y. Tomida, T.H. Rich & P. Vickers-Rich (eds), *Proceedings of the Second Gondwanan Dinosaur Symposium*. National Science Museum Monographs No. 15, Tokyo.

_____, & Coria, R. 2000. New specimen of *Giganotosaurus carolinii* (Coria & Salgado, 1995), supports it as the largest theropod ever found. *Gaia*, **15**: 117-122.

Chure, D. J. 1995. A reassessment of the gigantic theropod *Saurophagus maximus* from the Morrison Formation (Upper Jurassic) of Oklahoma, USA. *Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, **6**: 103-106.

_____. 2000. A new species of *Allosaurus* from the Morrison Formation of Dinosaur National Monument (UT-CO) and a revision of the theropod family Allosauridae. Ph.D. dissertation, Columbia University, New York, 964 pp.

_____. 2001. The wrist of *Allosaurus* (Saurischia: Theropoda), with observations on the carpus in theropods. Pp. 283-300 in J. Gauthier & L.F. Gall (eds), *New Perspectives on the Origin and Early Evolution of Birds*. Yale Peabody Museum, New Haven, CT.

_____, & Madsen, Jr, J. H. 1996. Variation in aspects of the tympanic system in a population of *Allosaurus fragilis* from the Morrison Formation (Upper Jurassic). *Journal of Vertebrate Paleontology*, **16**: 63-66.

Clyde, W. C. & Fisher, D. C. 1997. Comparing the fit of stratographic and morphologic data in phylogenetic analysis. *Paleobiology*, **23**: 1-19.

Colbert, E. H. 1989. The Triassic dinosaur *Coelophysis*. *Museum of Northern Arizona Bulletin*, **57**: 1-160.

Coria, R. A. & Currie, P. J. 2002. The braincase of *Giganotosaurus carolinii* (Dinosauria: Theropoda) from the Upper Cretaceous of Argentina. *Journal of Vertebrate Paleontology*, **22**: 802-811.

_____, & _____. 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas*, **28**: 71-118.

_____, & Salgado, L. 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature*, **377**: 224-226.

Currie, P. J. & Carpenter, K. 2000. A new specimen of *Acrocanthosaurus atokensis* (Theropoda, Dinosauria) from the Lower Cretaceous Antlers Formation (Lower Cretaceous, Aptian) of Oklahoma, USA. *Geodiversitas*, **22**: 207-246.

_____, & Chen, P.-J. 2001. Anatomy of *Sinosauropteryx prima* from Liaoning, northeastern China. *Canadian Journal of Earth Sciences*, **38**: 1705-1727.

_____, & Zhao, X.-J. 1993. A new large theropod (Dinosauria, Theropoda) from The Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2037-2081.

Depéret, C. & Savornin, J. 1927. La faune de reptiles et de poisons albiens de

Timimoun (Sahara algérien). *Bulletin de la société géologique de France*, **27**: 257-265.

de Queiroz, K. & Gauthier, J. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. *Systematic Zoology*, **39**: 307-322.

_____, & _____. 1992. Phylogenetic Taxonomy. *Annual Review of Ecology and Systematics*, **23**: 449-480.

Dong, Z. M., Zhang, Y. H., Li, X. & Zhou, S. W. 1978. Note on a new carnosaur, *Yangchuanosaurus shangyuensis* gen. et sp. nov. from the Jurassic of Yangchuan District, Sichuan Province. *Kexue Tongbao*, **23**: 298-302.

_____, Zhou, S. W. & Zhang, Y. H. 1983. The dinosaurian remains from Sichuan Basin, China. *Palaeontologica Sinica*, **162** (New Series C, No. 23): 1-145.

Fisher, D. C. 1992. Stratigraphic parsimony. Ppp.124-129 in W.P. Maddison & D.R. Maddison (eds), *MacClade: Analysis of Phylogeny and Character Evolution*, Version 3. Sinauer and Associates, Sunderland, MA.

Finarelli, J. A. & Clyde, W. C. 2002. Comparing the gap excess ratio and the retention index of the stratigraphic character. *Systematic Biology*, **51**: 166-176.

Forster, C. A. 1999. Gondwanan dinosaur evolution and biogeographic analysis. *Journal of African Earth Sciences*, **28**: 169-185.

Fox, D. L., Fisher, D. C. & Leighton, L. R. 1999. Reconstructing phylogeny with and without temporal data. *Science*, **284**: 1816-1819.

Franzosa, J. & Rowe, T. 2005. Cranial endocast of the Cretaceous theropod dinosaur *Acrocanthosaurus atokensis*. *Journal of Vertebrate Paleontology*, **25**: 859-864.

Galton, P. M. & Jensen, J. A. 1979. A new large theropod dinosaur from the Upper Jurassic of Colorado. Brigham Young University, Geology Studies 26:1-12.

Gao, Y. H. 1992. *Yangchuanosaurus hepingensis*-a new species of carnosaur from Zigong, Sichuan. *Vertebrata PalAsiatica*, **30**: 313-324.

Gates, T. A. 2005. The Late Jurassic Cleveland-Lloyd Dinosaur Quarry as a drought-Induced assemblage. *Palaios*, **20**: 363-375.

Gauthier, J., Kluge, A. G. & Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics*, **4**: 105-209.

Gheerbrant, E. & Rage, J.-C. 2006. Paleobiogeography of Africa: How distinct

Gondwana and Laurasia? *Palaeogeographhy, Palaeoclimatology, Palaeoecology*, **241**: 224-246.

Gradstein, F., Ogg, J. & Smith, A. 2004. *A Geologic Time Scale 2004*. Cambridge University Press, Cambridge.

Hanna, R. R. 2002. Multiple injury and infection in a sub-adult theropod dinosaur *Allosaurus fragilis* with comparisons to allosaur pathology in the Cleveland-Lloyd dinosaur quarry collection. *Journal of Vertebrate Paleontology*, **22**: 76-90.

Harris, J. D. 1998. A reanalysis of *Acrocanthosaurus atokensis*, its phylogenetic status, and Paleobiogeographic implications, based on a new specimen from Texas. *New Mexico Museum of Natural History and Science Bulletin*, **13**: 1-75.

Hitchin, R. & Benton, M. J. 1997. Stratigraphic indices and tree balance. *Systematic Biology*, **46**: 563-569.

Holtz, T. R. 1994. The phylogenetic position of the Tyrannosauridae: implications for theropod systematics. *Journal of Paleontology*, **68**: 1100-1117.

_____. 2000. A new phylogeny of the carnivorous dinosaurs. *Gaia*, **15**: 5-61.

_____, Molnar, R. E. & Currie, P. J. 2004. Basal Tetanurae. Ppp. 71-110 in D.B. Weishampel, P. Dodson & H. Osmolska (eds), *The Dinosauria* (2nd edition). University of California Press, Berkeley, California.

Huelsenbeck, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology*, **20**: 470-483.

Humphries, C. J. & Parenti, L. R. 1999. *Cladistic Biogeography* (2nd ed.). Oxford University Press, Oxford.

Hutt, S. 1999. *Neovenator salerii:* a new theropod dinosaur from the Wealden of the Isle of Wight: its status and significance for theropod evolution. MPhil. thesis, University of Portsmouth, Portsmouth, 196 pp.

_____, Martill, D. M. & Barker, M. J. 1996. The first European allosaurid dinosaur (Lower Cretaceous, Wealden Group, England). *Neues Jahrbuch fur Geologie und Palaeontologie Monatshefte*, **1996**: 635-644.

_____, Naish, D., Martill, D. M., Barker, M. J. & Newberry, P. 2001. A preliminary account of a new tyrannosauroid theropod from the Wessex Formation (Early Cretaceous) of southern England. *Cretaceous Research*, **22**: 227-242.

Hwang, S. H., Norell, M. A., Ji, Q. & Gao, K. 2004. A large compsognathid from the Early Cretaceous Yixian Formation of China. *Journal of Systematic Palaeontology*, **2**: 13-30.

Kitching, I. J., Forey, P. L., Humphries, C. H. & Williams, D. M. 1998. *Cladistics: The Theory and Practice of Parsimony Analysis*. The Systematics Association, London.

Larsson, H. C. E. 2001. Endocranial anatomy of *Carcharodontosaurus saharicus* (Theropoda: Allosauroidea) and its implications for theropod brain evolution. Pp.19-33 in D.H. Tanke & K. Carpenter (eds), *Mesozoic Vertebrate Life*. Indiana University Press, Bloomington, Indiana.

Le Loeuff, J. 1991. The Campano-Maastrichtian vertebrate faunas from southern Europe and their relationships with other faunas in the world; palaeobiogeographical implications. *Cretaceous Research*, **12**: 93-114.

Linnaeus, C. 1758. *Systema Naturae per Raegna Tria Naturae. Volume 1. Regnum Animale*. 10th [photographic facsimile] ed. Trustees, British Museum (Natural History), London, 823 pp.

Maddison, W. P. & Maddison, D. R. 2003. *MacClade*, Version 4.06. Sinauer and Associates, Sunderland, Mass.

Madsen, J. H. 1976. *Allosaurus fragilis*: a revised osteology. *Utah Geological Survey Bulletin*, **109**: 1-163.

Maganuco, S., Cau, A., Dal Sasso, C. & Pasini, G. 2007. Evidence of large theropods from the Middle Jurassic of the Mahajanga Basin, NW Madagascar,with implications for ceratosaurian pedal ungual evolution. *Atti Soc. It. Nat. Museo Civico Storia Naturale di Milano*, **148**: 261-271.

Marsh, O. C. 1877. Notice of new dinosaurian reptiles from the Jurassic Formation. *American Journal of Science* (Series 3), **14**: 514-516.

_____. 1878. Principal characters of American Jurassic dinosaurs. Pt. 1. *American Journal of Science* (Series 3), **16**: 411-416.

Mateus, O. 1998. *Lourinhanosaurus antunesi*, a new Upper Jurassic allosaurid (Dinosauria: Theropoda) from Lourinha, Portugal. *Memoirs of the Academy of Sciences, Lisbon*, **37**: 111-24.

_____, Walen, A. & Antunes, M. T. 2006. The larege theropod fauna of the Lourinha Formation (Portugal) and its similarity to that of the Morrison Formation, with a description of a new species of *Allosaurus*; Pp. 123-129 in Foster, J. R. & S. G. Lucas, (eds), *Paleontology and Geology of the Upper Jurassic Morrison Formation*. New Mexico Museum of Natural History and Science, Bulletin 36.

Naish, D., Hutt, S. & Martill, D. M. 2001. Saurischian dinosaurs 2: theropods; Pp. 252-309 in D.M. Martill & D. Naish (eds), *Dinosaurs of the Isle of Wight*. The Palaeontological Association.

_____, Martill, D. M. & Frey, E. 2004. Ecology, systematics, and biogeographical relationships of dinosaurs, including a new theropod, from the Santana Formation (?Albian, Early Cretaceous) of Brazil. *Historical Biology*, **2004**: 1-14.

Nelson, G. & Ladiges, P. Y. 1991. Three-area statements: standard assumptions for biogeographic analysis. *Systematic Zoology*, **40**: 470-485.

Norell, M. A. & Novacek, M. J. 1992. The fossil record and evolution: comparing cladistic and paleontologic evidence for vertebrate history. *Science*, **255**:1690-1693.

Novas, F. E. 1993. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. *Journal of Vertebrate Paleontology*, **13**:400-423.

_____. 1997. Abelisauridae; Pp.1-2 in P.J. Currie & K. Padian (eds), *Encyclopedia of Dinosaurs*. Academic Press, New York.

_____, de Valais, S., Vickers-Rich, P. & Rich, T. 2005. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften*, **92**: 226-230.

Ostrom, J. H. 1978. The osteology of *Compsognathus longipes* Wagner. *Zitteliana*, **4**: 73-118.

Padian, K. & Hutchinson, J. R. 1997. Allosauroidea; Pp.6-9 in P.J. Currie & K. Padian (eds), *Encyclopedia of Dinosaurs*. Academic Press, New York.

_____, _____, & Holtz, Jr, T. R. 1999. Phylogenetic definitions and nomenclature of the

major taxonomic categories of the carnivorous Dinosauria (Theropoda). *Journal of Vertebrate Paleontology*, **19**: 69-80.

Perez-Moreno, B. P., Chure, D.J., Pires, C., Marques da Sila, C., dos Santos, V., Dantas, P., Povoas, L., Cachao, M., Sanz, J. L. & Galopim de Carvalho, A. M. 1999. On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. *Journal of the Geological Society, London*, **156**: 449-452.

Platnick, N. I. & Nelson, G. 1981. A method of analysis for historical biogeography. *Systematic Zoology*, **27**: 1-16.

Pol, D. & Norell, M. A. 2001. Comments on the Manhattan Stratigraphic Measure. *Cladistics*, **17**: 285-289.

_____, _____ & Siddall, M.E. 2004. Measures of stratigraphic fit to phylogeny and their sensitivity to tree size, tree shape, and scale. *Cladistics*, **20**: 64-75.

Rabinowitz, P. D. & LaBrecque, J. 1979. The Mesozoic South Atlantic ocean and evolution of its continental margins. *Journal of Geophysical Research*, **84(B11)**: 5973-6002.

Rauhut, O. W. M. 1995. Zur systematischen Stellung der afrikanischen Theropoden *Carcharodontosaurus* Stromer 1931 und *Barhariasaurus* Stromer 1934. *Berliner Geowissenschaftliche Abhandlungen E*, **16** :357-375.

_____. 2003. The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology*, **69**: 1-213.

_____ & Fechner, R. 2005. Early development of the facial region in a non-avian theropod dinosaur. *Proceedings of the Royal Society, Series B*, **272**: 1179-1183.

Rayfield, E. J. 2005. Aspects of comparative cranial mechanics in the theropod dinosaurs *Coelophysis*, *Allosaurus*, and *Tyrannosaurus*. *Zoological Journal of the Linnean Society*, **144**: 309-316.

_____, Norman, D. B., Horner, C. C., Horner, J. R., May Smith, P., Thomason, J. J. & Upchurch, P. 2001. Cranial design and function in a large theropod dinosaur. *Nature*, **409**: 1033-1037.

Rowe, T. 1989. A new species of the theropod dinosaur *Syntarsus* from the Early

Jurassic Kayenta Formation of Arizona. *Journal of Vertebrate Paleontology*, **9**: 125-136.

Sampson, S. D., Witmer, L. M., Forster, C. A., Krause, D. W., O'Connor, P. M., Dodson, P. & Ravoavy, F. 1998. Predatory dinosaur remains from Madagascar: implications for the Cretaceous biogeography of Gondwana. *Science*, **280**: 1048-1051.

Scotese, C. R. 2004. Cenozoic and Mesozoic paleogeography: changing terrestrial biogeographic pathways. Pp.9-26 in M.V. Lomolino & L.R. Heaney (eds), *Frontiers of Biogeography: New Directions in the Geography of Nature*. Sinauer and Associates, Sunderland, MA.

Sereno, P. C. 1993. The pectoral girdle and forelimb of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleongology*, **13**: 425-450.

_____. 1997. The origin and evolution of dinosaurs. *Annual Review of Earth and Planetary Sciences*, **25**: 435-489.

_____. 1998. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, **210**: 41-83.

_____. 1999a. The evolution of dinosaurs. *Science*, **284**: 2137-2147.

_____. 1999b. Dinosaurian biogeography: vicariance, dispersal and regional extinction. Pp. 249-257 in Y. Tomida, T.H. Rich & P. Vickers-Rich (eds), *Proceedings of the Second Gondwanan Dinosaur Symposium*. National Science Museum Monographs No. 15, Tokyo.

_____. 2004. CharacterSearch: online database for characters. *Journal of Vertebrate Paleontology*, **24(3)**: 112A.

_____. 2005. *Stem Archosauria—TaxonSearch*. URL http://www.taxonsearch.org/dev/file_home.php [version 1.0, 2005 November 7, linked to Sereno et al. 2005 reference below]

_____. In press. Logical basis for morphological characters in phylogenetics. *Cladistics*.

_____, **& Brusatte, S. L.** In press. Basal abelisaurid and carcharodontosaurid theropods

from the Elrhaz Formation (Aptian-Albian) of Niger. *Acta Palaeontologica Polonica*.

_____ & _____. Submitted. The tyrannosaur tree: a status report. In M. Henderson *et al*. (eds), *The Origin, Systematics, and Paleobiology of Tyrannosauridae*. Northern Illinois University Press, DeKalb, IL.

_____ & Novas, F. E. 1993. The skull and neck of the basal theropod *Herrerasaurus ischigualastensis*. *Journal of Vertebrate Paleontology*, **13**: 451-476.

_____, McAllister, S. & Brusatte, S. L. 2005. *TaxonSearch*: a relational database for suprageneric taxa and phylogenetic definitions. *Phyloinformatics*, **8**: 1-21.

_____, Wilson, J. A. & Conrad, J. L. 2004. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proceedings of the Royal Society, Series B,* **271**: 1325-1330.

_____, Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., Sidor, C. A., Varricchio, D. J. & Wilson, J. A. 1996. Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science,* **272**: 986-991.

Siddall, M. E. 1996. Stratigraphic consistency and the shape of things. *Systematic Biology*, **45**: 111-115.

_____. 1997. Stratigraphic indices in the balance: a reply to Hitchin and Benton. *Systematic Biology*, **46**: 569-573.

_____. 1998. Stratigraphic fit to phylogenies: a proposed solution. *Cladistics*, **14**: 201-208.

Smith, A. G., Smith, D. G. & Funnell, B. M. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press, Cambridge.

Smith, D. K. 1998. A morphometric analysis of *Allosaurus*. *Journal of Vertebrate Paleontology*, **18**: 126-142.

_____. & Lisak, F. J. 2001. An unusual specimen of *Allosaurus* from Southeastern Utah. *Brigham Young University Geology Studies*, **46**: 93-98.

_____, Richmond, D. R. & Bybee, P. J. 1999. Morphological variation in a large specimen of *Allosaurus fragilis*, Upper Jurassic Morrison Formation, Eastern Utah. Pp. 135-141 in D.D. Gillette (ed), *Vertebrate Paleontology in Utah*. Utah Geological Survey.

Smith, N., Hammer, W. & Currie, P. 2005. Osteology and phylogenetic relationships of *Cryolophosaurus ellioti* (Dinosauria: Theropoda): implications for basal theropod evolution. *Journal of Vertebrate Paleontology*, **25**: 116A-117A.

Stovall, J. W. & Langston, W. 1950. *Acrocanthosaurus atokensis*, a new genus and species of Lower Cretaceous Theropoda from Oklahoma. *American Midland Naturalist*, **43**: 696-728.

Stromer, E. 1931. Ergebnisse der Forschungsrisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharje-Stufe (unterstes Cenoman). 10. Ein Skelett-Rest von Carcharodontosaurus no. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge*, **9**: 1-23.

_____. 1934. Ergebnisse der Forschungsreisen Prof E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharje-Stufe (unterstes Cenoman). 13. Dinosauria von E. Stromer. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge*, **22**: 1-79.

Sumrall, C. D. & Brochu, C. A. 2003. Resolution, sampling, higher taxa and assumptions in stratocladistic analysis. *Journal of Paleontology*, **77**: 189-194.

Swofford, D. L. 2000. *PAUP*: Phylogenetic Analysis Using Parsimony* (*and other methods), Version 4.10b. Released by the author.

Tykoski, R. S. & Rowe, T. 2004. Ceratosauria. Pp.47-70 in D.B. Weishampel, P. Dodson & H. Osmolska (eds), *The Dinosauria* (2nd edition). University of California Press, Berkeley, California.

Upchurch, P., Hunn, C. A. & Norman, D. B. 2002. An analysis of dinosaurian biogeography: evidence for the existence of vicariance and dispersal patterns caused by geological events. *Proceedings of the Royal Society of London, Series B*, **269**: 613-621.

Wagner, P. J. & Sidor, C. A. 2000. Age rank/clade rank metrics—sampling, taxonomy, and the meaning of "stratigraphic consistency." *Systematic Biology*, **49**: 463-479.

Weishampel, D. B., Barrett, P. M., Coria, R. A., Le Loeuff, J., Xu, X., Zhao, X., Sahni, A., Gomani, E. M. P. & Noto, C. R. 2004. Dinosaur Distribution. Pp. 517-606 in D.B. Weishampel, P. Dodson & H. Osmolska (eds), *The Dinosauria* (2nd edition). University of California Press, Berkeley, California.

Wilkinson, M. 1995. Coping with abundant missing entries in phylogenetic inference using parsimony. *Systematic Biology*, **44**: 501-514.

Wills, M. A. 1999. Congruence between phylogeny and stratigraphy: randomization tests and the gap excess ratio. *Systematic Biology*, **48**: 559-580.

Wilson, J. A. 2005. Integrating ichnofossil and body fossil records to estimate locomotor posture and spatiotemporal distribution of early sauropod dinosaurs: a stratocladistic approach. *Paleobiology*, **31**: 400-423.

Xu, X., Norell, M. A., Kuang, X., Wang, X., Zhao, Q. & Jia, C. 2004. Basal tyrannosauroids from China and evidence for protofeathers in tyrannosauroids. *Nature*, **431**: 680-684.

_____, Clark, J. M., Forster, C. A., Norell, M. A., Erickson, G. M., Eberth, D. A., Jia, C. & Zhao, Q. 2006. A basal tyrannosauroid dinosaur from the Late Jurassic of China. *Nature*, **439**: 715-718.

Zhao, X.-J. & Currie, P. J. 1993. A large crested theropod from the Jurassic of Xinjiang, People's Republic of China. *Canadian Journal of Earth Sciences*, **30**: 2027-2036.

APPENDIX 1
CHARACTER LIST AND DESCRIPTIONS

Characters and character states are listed below along with citation of their first use in the cladistic literature. Several of the characters that involve the presence or absence of a feature as well as its variation (characters 6-8, 10, 12, 13, 25-28, 47) are better coded as independent characters (Sereno in press) but were left as single characters here for ease of comparison to character data in previous studies.

1. External naris, long axis length: less (0) or more (1) than 50 percent anteroposterior diameter of the orbit. (modified from Holtz *et al*. 2004:51)
2. Premaxilla, number of teeth: three or four (0); five (1). (Harris 1998:47)
3. Premaxilla, main body, proportions: anteroposteriorly longer than dorsoventrally deep (0); approximately as long as deep (1); deep than long (2). (modified from Holtz 2000:5)
4. Premaxilla, ventral portion of anterior margin, inclination: vertical (0); inclined slightly posterodorsally (1). (New character)
5. Maxilla, antorbital fenestra, ventral margin, position of the medial rim: lower than (0) or level with (1) lateral rim. (modified from Holtz *et al*. 2004:36)
6. Maxilla, promaxillary fenestra, lateral exposure: absent, no fenestra (0); fully exposed (1); present, obscured by the lateral lamina of the ascending ramus (2). (modified from Harris 1998:2)
7. Maxilla, promaxillary fenestra, orientation: absent or laterally facing (0); anteriorly facing (1). (Holtz *et al*. 2004:38)
8. Maxilla, maxillary fenestra, position relative to the anterior corner of the antorbital fossa: absent or anterior margin terminates posterior to the anterior margin of the antorbital fossa (0); terminates along the anterior margin of the antorbital fossa (1). (Holtz *et al*. 2004:43)
9. Maxilla, pneumatic excavation on the medial lamina of the ascending ramus: absent (0); present (1). (Harris 1998:2)
10. Maxilla, promaxillary recess, form of medial wall: recess absent or small (0); solid (1); fenestrated, open medially (2). (modified from Allain 2002:5)

11. Maxilla, articular surface with the premaxilla, inclination in lateral view: angled strongly posterodorsally (0); subvertical (1). (New character)
12. Maxilla, lateral lamina of ascending ramus, form: absent or present as a slightly overhanging crest (0); present as a large shelf overlapping the anterior part of the antorbital fossa (1). (Holtz *et al*. 2004:39)
13. Maxilla, external sculpturing, extent: absent or present and restricted to the anterior and lateral margins above the tooth row (0); present and extensively covering the main body of the maxilla (1). (Forster 1999:11)
14. Maxilla, posterior interdental plates: separate (0); fully coossified (1). (Forster 1999:3)
15. Maxilla, anterior interdental plates, dorsoventral depth: less (0) or more (1) than twice anteroposterior width. (New character)
16. Nasal, dorsal surface, form: low texture (0); heavily rugose (1). (Forster 1999:11)
17. Nasal, shape in dorsal view: expanding posteriorly, so that the lateral margins diverge (0); parallel-sided throughout its length (1). (modified from Rauhut 2003:21)
18. Nasal, lateral margin, form: flat (0); offset with a small lateral crest (1). (modified from Rauhut 2003:22)
19. Nasal, shape of the posterior suture: medial projection extends as far or farther posteriorly than the lateral projection (0); lateral projection extends farther posteriorly than the medial projection (1). (Holtz *et al*. 2004:56)
20. Lacrimal, dorsal surface, form: unpronounced, level with or only slightly raised above skull roof (0); rugose, with a raised crest or a pronounced horn (1). (Harris 1998:11)
21. Lacrimal, posterior surface, form: smoothly concave (0); marked by a prominent projecting suborbital flange (1). (Currie & Carpenter 2000:19)
22. Postorbital, ventral process, orientation: subvertical (0); angled anteroventrally (1). (Holtz *et al*. 2004:104)
23. Postorbital, suborbital flange on ventral process, form: absent or indistinct (0); present as a discrete projection on the ventral ramus (1). (Sereno *et al*. 1996:49)
24. Postorbital, ventral tip of the ventral process, extent: nearly as ventral as the ventralmost margin of orbit and clearly ventral to the squamosal-quadratojugal contact (0); well dorsal to the ventralmost margin of the orbit and at

approximately the same level as the squamosal-quadratojugal contact (1). (Harris 1998:7)

25. Postorbital, dorsal surface, form: smooth (0); convex rugosity (1); anteriorly-projecting rugosity (2). (Holtz 2000:52)
26. Postorbital, dorsal boss, size: absent or only slightly overhanging orbit (0); bulbous swelling extensively overhanging orbit (1). (New character)
27. Jugal, antorbital fossa, form: absent or developed as a slight, narrow depression (0); present and developed as a large, extensive depression (1). (modified from Holtz *et al*. 2004:116)
28. Jugal, pneumatization: absent or shallow (0); extensive, invaginated recess externally (1). (modified from Harris 1998:12)
29. Squamosal, ventral (=precotyloid) process, flange into lateral temporal fenestra: absent (0); present (1). (Holtz 2000:57)
30. Squamosal, ventral (=precotyloid) process, length relative to the posterior (=postcotyloid) process in lateral view: longer (0); subequal (1). (New character)
31. Prefrontal: present as a distinct element (0); absent, lost or coossified with the lacrimal or frontal and not visibly distinct (1). (New character)
32. Frontal, supratemporal fossa, exposure in dorsal view: broadly exposed on frontal (0); mostly hidden, restricted by overhanging frontoparietal shelf (1). (modified from Coria & Currie 2002:1)
33. Frontal, anteromedial corner of the supratemporal fossa, form: open dorsally (0); roofed over by a frontoparietal shelf (1). (Forster 1999:33)
34. Frontal, interfrontal suture: open (0); coossified (1). (Holtz 2000:41)
35. Frontal, suture with parietal: open (0); coossified (1). (Forster 1999:38)
36. Frontal, contribution to the orbital rim: present (0); absent, excluded by lacrimal-postorbital contact (1). (Sereno *et al*. 1996:48)
37. Parietal, nuchal plate, orientation with respect to frontal-parietal-postorbital suture: not parallel (0); parallel (1). (modified from Coria & Currie 2002:10)
38. Parietal, posteriorly-placed knob-like dorsal projection, form: absent or very low(0); pronounced (1). (modified from Rauhut 2003:42)
39. Braincase, basal tubera, transverse width relative to that of the occipital condyle:

greater (0); less (1). (Holtz 2000:97)

40. Braincase, occipital condyle, shape: subspherical (0); dorsoventrally compressed (1). (Coria & Currie 2002:15)
41. Braincase, neck of occipital condyle, paired pneumatic openings that join in midline: absent (0); present (1). (modified from Coria & Currie 2002:6)
42. Braincase, angle between the axis of the occipital condyle and the transverse plane of the basal tubera: approximately 90 degrees (0); less than 75 degrees (1). (modified from Forster 1999:43)
43. Braincase, ossification of the interorbital septum: absent (0); present (1). (modified from Coria & Currie 2002:4)
44. Braincase, trigeminal (nerve V) foramen, location relative to nuchal crest: anterior or ventral (0); posterior (1). (Coria & Currie 2002:2)
45. Braincase, supratemporal fenestrae, orientation: dorsal (0); anterolateral (1). (Coria & Currie 2002:9)
46. Braincase, basal tubera, composition: formed equally by the basioccipital and basisphenoid and not subdivided (0); subdivided by a lateral longitudinal groove into a medial part entirely formed by the basioccipital and a lateral part entirely formed by the basisphenoid (1). (Sereno *et al*. 1996:44)
47. Palatine, pneumatic recess, form: absent or small foramen (0); large fossa with one or more foramina (1). (Harris 1998:33)
48. Lower jaw, external mandibular fenestra, size: large (0); small (1). (Harris 1998:38)
49. Dentary, anterior end, shape: rounded (0); squared and expanded (1). (Sereno *et al*. 1996:50)
50. Dentary, anteroventral margin, form: smooth, convex (0); marked by a projecting flange, forming a “dentary chin” (1). (New character)
51. Dentary, posterior end of principal neurovascular foramina row, location: parallels the tooth row (0); curves ventrally as it extends posteriorly (1). (New character)
52. Dentary, external surface, texture: smooth (0); rugose, marked by prounounced lineations and ridges (1). (New character)
53. Dentary, symphysis, angle in dorsal view: low, acute angle, tooth row forms V-

shaped convergence (0); high, obtuse angle, tooth row forms U-shaped convergence (1). (New character).

54. Dentary, orientation of dorsal and ventral margins of the tooth-bearing section: subparallel (0); caudally divergent (1). (Holtz *et al*. 2004:219)
55. Dentary, posterior end, form: strongly forked (0); slightly forked or straight (1). (Rauhut 2003:77)
56. Surangular, dorsoventral depth over the external mandibular fenestra: less (0) or more than (1) half the depth of the mandible. (Sereno *et al*. 1996:47)
57. Surangular, anterior ramus, depth relative to the depth of the surangular and angular under the latertemporal fenestra: less (0) or more than (1) 50%. (Forster 1999:8)
58. Articular, retroarticular process, form: long, narrow, and rod-like (0); broadened, with a posterior groove (1). (Holtz *et al*. 2004:249)
59. Maxillary and dentary teeth in center of tooth rows, profile of posterior margin (away from the tip): concave (0); straight, crown recurvature absent (1). (modified from Holtz *et al*. 2004:265)
60. Axis, ventral margin of the axial intercentrum, orientation relative to the ventral margin of the axial centrum: approximately parallel (0); angled strongly dorsally (1). (Harris 1998:50)
61. Axis, ventral keel: present (0); absent (1). (Harris 1998:51)
62. Cervicals, posterior articular face of mid cervical centra, width: approximately as broad as tall (0); at least 20% broader than tall (1). (Sereno *et al*. 1996:53)
63. Cervicals, anterior articular face of mid cervical centra, orientation relative to posterior face: elevated (0); approximately at same level (1). (Sereno *et al*. 1996:54)
64. Cervicals, interior structure of centrum, pneumaticity: apneumatic or camerate (simple) (0); camellate (complex) (1). (Harris 1998:62)
65. Cervicals, pleurocoels on postaxial cervicals, form: absent or single opening (0); multiple openings within in a single fossa (1). (Harris 1998:61)
66. Cervicals, location of the zygapophyses relative to the midline: over centrum (0); displaced lateral to centrum (1). (modified from Holtz 2000:155)
67. Dorsals, pleurocoels, distribution: absent or restricted to the anterior dorsals (0);

present on all dorsals (1). (Harris 1998:66)

68. Dorals, posterior centra, anteroposterior length: approximately equal to or longer than dorsoventral depth (0); shorter than deep (1). (Holtz *et al*. 2004:337)
69. Dorsals, neural spines, height relative to centrum: less (0) or more (1) than twice centrum height. (Holtz 2000:167)
70. Dorsals, centrum, shape relative to mid section height: subcylindrical, the dorsoventral thickness of the central section greater than 60% the height of the cranial face (0); hourglass-shaped, the dorsoventral thickness less than 60% the height of the cranial face (1). (Holtz 2000:175)
71. Sacrals, pleurocoels: absent (0); present (1). (Harris 1998:70)
72. Caudals, rudimentary pleurocoels: absent (or as shallow fossa) (0); present (1). (Sereno *et al*. 1996:55)
73. Caudals, distal caudal prezygapophyses, length: more (0) or less (1) than 40% overlap of the preceding vertebral body. (Holtz 2000:199)
74. Gastralia, distal end of medial element, shape: tapered (0); club-shaped prominence (1). (New character)
75. Gastralia, number of sets of fused medial elements: zero or one (0); greater than one (1). (New character)
76. Ilium, posterior margin or postacetabular process, profile: gently convex or posteriorly tapering (0); straight along its entire margin (1). (New character)
77. Ilium, anterior margin of preacetabular process, profile: gently convex (0); straight (1). (New character)
78. Ilium, pubic peduncle, position relative to the preacetabular process: anterior margin located posterior to (0), or even with (1), the anterior margin of the preacetabular process. (New character)
79. Pubis, pubic boot, anterior expansion: absent or weakly developed (0); expanded (1). (Harris 1998:113)
80. Pubis, pubic boot, size relative to pubic length: less than 50% (0); 50-60% (1); greater than 60% (2). (Sereno *et al*. 1996:51)
81. Ischium, distal end, form: confluent with shaft or only slightly expanded (0); strongly

expanded into distinct boot, with anterior and posterior projections (1). (Harris 1998:119)

82. Ischium, posteriorly-directed flange on iliac peduncle: absent (0); present (1). (New character)
83. Femur, orientation of central axis of head to shaft in anterior view: approximately perpendicular (0); angled dorsally, resulting in an obtuse angle between the head and the shaft (1). (Harris 1998:121)
84. Femur, lateral distal condyle, form: bulbous (0); cone-shaped (1). (New character)
85. Femur, medial epicondyle (=mediodistal crest), length: poorly developed or short (0); pronounced, extending 30% or more up the length of the femoral shaft (1). (Holtz *et al*. 2004:574)
86. Femur, fourth trochanter, form: robust or completely absent (0); present but reduced to a weak crest (1). (Harris 1998:126)
87. Femur, extensor groove on distal end, form: deep and narrow (0); shallow and broad (1). (Harris 1998:127)
88. Femur, ridge for cruciate ligaments in flexor groove, form: absent or indistinct (0); present and robust (1). (Harris 1998:128)
89. Tibia, lateral condyle separation from remainder of proximal end in proximal view: bulging from the main surface of the tibia (0); conspicuous narrowing between the body of the condyle and the main body of the tibia (1). (modified from Azuma & Currie 2000:108)
90. Tibia, medial malleolus, medial expansion: only slightly expanded medially (0); expanded 9% or more the length of the tibia (1). (New character)
91. Tibia, lateral malleolus, distal extension relative to medial malleolus: even with or extends slightly distally (0); extent beyond the medial malleolus 7% or more the length of the tibia (1). (New character)
92. Fibula, length relative to femur: greater (0) or less than (1) 70%. (New character)
93. Astragalus, height of ascending process relative to tibial length: less than 1/6 (0); between 1/6 and 1/4 (or greater than 1/4 in Compsognathidae) (1). (Harris 1998:135)
94. Scapulocoracoid, notch between scapular acromion process and coracoid:

absent (0); present (1). (Currie & Carpenter 2000:68)

95. Coracoid, posteroventral process, length relative to the width of the glenoid: shorter (0); longer, process strongly hooked (1). (Sereno *et al*. 1996:28)

96. Scapula, acromion process, size: prominent (0); reduced or absent (1). (Holtz 2000:213)

97. Scapula, blade, length relative to minimum neck width: more (0) or less than (1) 7.5. (Forster 1999:63)

98. Metacarpal 4: present (0); absent (1). (Harris 1998:100)

99. Metacarpals, proximal articular ends, transverse width: less (0) or two times or more (1) than minimum transverse shaft width. (New character)

Stratigraphic Character. Bathonian-Oxfordian or older (0); Kimmeridgian-Tithonian (1); Barremian (2); Early Aptian (3); Late Aptian-Cenomanian or younger (4).

APPENDIX 2
DATA MATRIX

OUTGROUPS
Herrerasaurus 0000000000 0000000010 0000000000 0000000001 0000000000
0000000000 0000000000 0000000100 0000000000 0000001000

Coelophysis 0000000000 0000?00100 0001000000 0000000000
00?0000000 ?000000000 0000?00000 001??00000 0000000000 0000000000

Torvosaurus 0020000000 00010????? ?000100??? ?????0???? ????????00
00??????0? ?0000?1000 ?00??0?000 00???00?01 1?0????101

Compsognathidae 00000??002 0000?000?0 000100000?
0?00000?0? ?????0?100 ?0?0?1100? ??0??10000 0000000000 000?01???0 0010000101

INGROUP
Acrocanthosaurus 002101000? 000??01011 1111211111 0001110110
0000001111 ?011111100 0111101010 11111???12 1110100111 11?1110114

Allosaurus 1110021112 1101000101 0001100011 0000000010 0000010100 0001111101
1000010101 0000011111 0100100110 0011100101

Carcharodontosaurus 1???1???01 0011111000 11112111?? 1111111100 111110??11
111?????1? ?11100???? ?1?1?????? ?111100??? ?1???????4

Eocarcharia ????11001?
00010????? ?11121???? ?00111???? ?????????? ????????0? ?????????? ?????????? ?????
????? ?????????4

Giganotosaurus ?021?2110? 0011111O?1 111121???? 11111111?1 11111???11
1110????11 00111?1?00 ?1111???12 0111111011 0111111??4

Mapusaurus ????1??10? 0011111O?0 11??2111??
1????????? ????????11 ?1?0???11? ??????11?? 111??000?? 0111111O?1 1?11?10?14

Neovenator 1111021101 110100100? ?????????? ?????????? ??????1?00 100?????00
1001101001 0000?0?012 1011100?10 101?1?0??2

Sinraptor 1000010012 0000000111 1002201100 0000001111 0100111000 0001000001
1000010011 00?0?11100 0000000100 0000001000

Tyrannotitan ?????????? ?????????? ?????????? ?????????? ????????10 ?110????0? ????
111?00 00????0??? 0?1?1????? ?1??1?0??3

Fukuiraptor ?????????? ???10????? ?????????? ?????????? ????????00 ?00?????0? ????? ?00?0 ?????????? ??001000?? ????1????x

Monolophosaurus 10101???0? 100??10101 0000000110 0000000101 ?0??00?100 0000111001 ?00?010110 ?0????1000 00???????? ???0?????x

APPENDIX 3
SCORING SOURCES

Herrerasaurus: PVSJ 407 (original material and cast); Novas 1993; Sereno 1993; Sereno and Novas 1993
Coelophysis: Colbert 1989; Rowe 1989; Tykoski & Rowe 2004; Bristowe & Raath 2004
Torvosaurus: UUVP cast material; Galton & Jensen 1979; Britt 1991
Compsognathidae: Ostrom 1978; Currie & Chen 2001; Hwang *et al*. 2004; Naish *et al*. 2004
Acrocanthosaurus: OMNH 10146, OMNH 10147, NCSM 14345 (original material); Stovall & Langston 1950; Harris 1998; Currie & Carpenter 2000; Franzosa & Rowe 2005
Allosaurus: UUVP/UMNH VP original and cast material (numerous specimen numbers, skull and forelimbs); Madsen 1976; Chure 2000; Chure 2001
Carcharodontosaurus: *C. saharicus*: SGM-Din 1 (neotype skull), SGM-Din 3, 4, 5 (cervical vertebrae), numerous UCRC uncataloged elements; *C. iguidensis*: MNN IGU2 (holotype maxilla), MNN IGU3 (braincase), MNN IGU 4 (lacrimal), MNN IGU5 (dentary), MNN IGU6, 7, 8, 9, 10 (isolated teeth) (original material); Stromer 1931; Stromer 1934; Rauhut 1995; Sereno *et al*. 1996; Larsson 2001; Brusatte & Sereno 2005, in press a
Eocarcharia: MNN GAD2, 3, 4, 5, 6 (postorbitals), MNN GAD 7, 8, 9 (maxillae), MNN GAD 10, 11 (frontal and prefrontal); MNN GAD12, 13, 14 (teeth) (original material); Sereno & Brusatte in press
Giganotosaurus: MUCPv-CH1 (original material); Coria & Salgado 1995; Calvo 1999; Calvo & Coria 2000; Coria & Currie 2002
Mapusaurus: Coria & Currie 2006
Neovenator: MIWG 5470, 6348, 5470; BMNH R1001 (original material); Hutt *et al*. 1996; Hutt 1999 (unpublished thesis); Naish *et al*. 2001
Sinraptor: IVPP 10600 (original material); Gao 1992; Currie & Zhao 1993
Tyrannotitan: Novas *et al*. 2005
Fukuiraptor: Azuma & Currie 2000
Monolophosaurus: IVPP 84019 (original material); Zhao & Currie 1993

SUPPLEMENTARY APPENDIX 1
SYNAPOMORPHY LIST
Note: “r” designates a reversal

***Allosaurus* + Carcharodontosauridae**
ACCTRAN: 2,3,6(2),7,8,11,12,14,29,30,55,58,79,80,82,85,89,94,95
DELTRAN: 3,6(2),7,8,14,19r,29,30,40r,48,55,56,57,58,79,85,89,93,94,95
All: 3,6(2),7,8,14,29,30,55,58,79,85,89,94,95

Carcharodontosauridae
ACCTRAN:
4,9r,10r,17,18r,22,23,26,34,35,36,46r,51,54r,60r,64,65,66r,67,75,76r,77r,78r,80(2),83,84,
91,96,99
DELTRAN: 4,10r,17,47,51,64,65,67,80(2),83,91
All: 4,10r,17,51,64,65,67,80(2),83,91

***Tyrannotitan* + more derived carcharodontosaurids**
ACCTRAN: 2,3(2),5,11r,12r,49,52,53,61r,62,63,70r,73,74,90,92
DELTRAN:49,53,70r,92
All: 49,53,70r,92

***Acrocanthosaurus* + *Eocarcharia* + Carcharodontosaurinae**
ACCTRAN: 50,71,72
DELTRAN:
3(2),21,22,23,26,27,28,34,35,36,38,50,61r,63,66r,71,72,73,74,75,82,90,96,99
All: 50,71,72

Acrocanthosaurus* + *Eocarcharia
ACCTRAN: 1r,6r,7r,8r,19,52r,54,69,81,84r
DELTRAN: 6r,7r,8r
All: 6r,7r,8r

Carcharodontosaurinae
ACCTRAN: 13,15,16,20r,31,32,33,37,39r,41,42,43,44,45,59,60,68,88r
DELTRAN: 5,13,15,16,31,32,33,37,41,42,43,44,45,52,59,84
All: 13,15,16,31,32,33,37,41,42,43,44,45,59

Giganotosaurini (*Giganotosaurus* + *Mapusaurus*)
ACCTRAN: 40,62r,86,87
DELTRAN: 86,87,88r
All: 86,87

SUPPLEMENTARY APPENDIX 2

A list of scoring differences between this analysis and the analyses of Currie & Carpenter (2000), Allain (2002), and Novas *et al*. (2005). Character numbers from the original analyses are given at left, and denoted by C (Currie & Carpenter 2000), A (Allain 2002), and N (Novas *et al*. 2005). Scores favoured by the current analysis are denoted by B (Brusatte & Sereno). Alternative scores are given at right

Currie & Carpenter (2000)

C3 *Carcharodontosaurus* (C=1, B=?); *Giganotosaurus* (C=1, B=2)
C4 *Acrocanthosaurus* (C=0, B=1)
C10 *Giganotosaurus* (C=?, B=0)
C12 *Acrocanthosaurus* (C=0, B=1)
C14 *Carcharodontosaurus* (C=1, B=0)
C19 *Giganotosaurus* (C=0, B=1); *Carcharodontosaurus* (C=0, B=1)
C24 *Acrocanthosaurus* (C=1, B=0); *Sinraptor* (C=0, B=1), *Giganotosaurus* (C=0, B=?)
C37 *Acrocanthosaurus* (C=?, B=1); *Allosaurus* (C=0, B=1)
C44 *Allosaurus* (C=0, B=1)
C50 *Acrocanthosaurus* (C=0, B=1)
C53 *Carcharodontosaurus* (C=?, B=2); *Giganotosaurus* (C=?, B=2)
C57 *Giganotosaurus* (C=1, B=2)
C61 *Acrocanthosaurus* (C=0, B=1); *Carcharodontosaurus* (C=0, B=1); *Giganotosaurus* (C=0, B=1).
C68 *Giganotosaurus* (C=?, B=1); *Sinraptor* (C=?, B=0)
C86 *Acrocanthosaurus* (C=2, B=1/2); *Allosaurus* (C=2, B=1)
C97 *Acrocanthosaurus* (C=1, B=2)
C102 *Giganotosaurus* (C=0, B=1)
C103 *Giganotosaurus* (C=?, B=1)
C104 *Giganotosaurus* (C=?, B=0)
C109 *Acrocanthosaurus* (C=1, B=?)

Allain (2002)

A1 *Giganotosaurus* (A=0, B=1)
A5 *Acrocanthosaurus* (A=3, B=?); *Giganotosaurus* (A=2, B=?)
A33 *Carcharodontosaurus* (A=?, B=0)
A39 *Acrocanthosaurus* (A=0, B=1)
A41 *Carcharodontosaurus* (A=0, B=?); *Giganotosaurus* (A=0, B=?)

Novas *et al*. (2005)

N1 *Carcharodontosaurus* (N=1, B=?); *Giganotosaurus* (N=1, B=2)
N2 *Acrocanthosaurus* (N=0, B=1)
N9 *Acrocanthosaurus* (N=0, B=1); *Sinraptor* (N=1, B=0)

N11 *Carcharodontosaurus* (N=1, B=0)
N24 *Sinraptor* (N=1, B=0)
N25 *Acrocanthosaurus* (N=0, B=1); *Carcharodontosaurus* (N=?, B=1)
N28 *Allosaurus* (N=0, B=1)
N32 *Carcharodontosaurus* (N=?, B=1)
N44 *Giganotosaurus* (N=0, B=1); *Sinraptor* (N=?, B=0)
N56 *Acrocanthosaurus* (N=2, B=1/2); *Allosaurus* (N=2, B=1); *Tyrannotitan* (N=2, B=1)
N66 *Acrocanthosaurus* (N=1, B=2)
N71 *Giganotosaurus* (N=0, B=1); *Tyrannotitan* (N=0, B=?)
N72 *Giganotosaurus* (N=?, B=1); *Tyrannotitan* (N=2, B=?)
N73 *Giganotosaurus* (N=?, B=0); *Tyrannotitan* (N=1, B=?)
N75 *Acrocanthosaurus* (N=1, B=?)
N78 *Acrocanthosaurus* (N=1, B=0); *Giganotosaurus* (N=0, B=?); *Sinraptor* (N=0, B=1)
N99 *Acrocanthosaurus* (N=1, B=0); *Sinraptor* (N=0, B=1)

SUPPLEMENTARY APPENDIX 3

A list of informative characters from the analyses of Currie & Carpenter (2000), Allain (2002), and Novas *et al*. (2005) rejected by this study, along with reasons for rejection, followed by a list of rejected characters from other analyses. Numbers denote the number of the character in the original analysis in question.

Currie & Carpenter (2000)
Redundant: 16
Miscoding: 64
Too Variable: 28, 62, 85, 95
Poorly Defined/Not Quantified: 23, 26, 27, 29, 30, 42, 46, 100
Total: 14 rejected characters

Allain (2002)
Redundant: n/a
Miscoding: 6, 20
Too Variable: n/a
Poorly Defined/Not Quantified: 23, 32, 42
Total: 5 rejected characters

Novas *et al*. (2005)
Redundant: 17, 76, 92
Miscoding: 22, 41, 54, 74, 87, 89
Too Variable: 19, 40
Poorly Defined/Not Quantified: 20, 26, 27, 29, 36, 38, 57, 77, 79, 80, 97
Total: 22 rejected characters

Sereno *et al*. 1996: 41, 42, 52
Harris 1998: 13, 27, 28, 52, 65, 73
Forster 1999: 10, 28, 32, 37, 39, 40, 42, 80, 81, 85
Azuma & Currie 2000: 2, 8, 15, 34, 41, 48, 68, 100
Holtz 2000: 8, 9, 10, 13, 14, 15, 17, 23, 33, 58, 62, 87, 88, 99, 100, 103, 112, 130, 131, 147, 166, 169, 178, 212, 214, 302, 318, 332, 331, 350
Coria & Currie 2002: 3, 5, 8, 13
Rauhut 2003: 6, 11, 17, 177
Holtz *et al*. 2004: 19, 27, 28, 30, 32, 34, 40, 62, 80, 83, 122, 123, 130, 131, 156, 166, 167, 168, 170, 199, 232, 238, 252, 256, 264, 286, 305, 355, 386, 388, 393, 461, 493, 499, 515, 519, 520, 533, 535, 544, 556, 558, 565, 572, 619, 626
Coria & Currie 2006: 9, 16, 18, 23, 26, 29, 30, 46, 47, 58, 62, 64, 69, 72, 76, 84, 85, 87, 99, 100, 110

SUPPLEMENTARY APPENDIX 4

A list of scores for *Neovenator* for the analyses of Currie & Carpenter (2000), Allain (2002), and Novas *et al*. (2005).

Currie & Carpenter (2000):
012?1 010?? ????? ????? ????? ????? ????? ????? ????? ?0?0? ?1200 02121 12??0 02?11 ?1?10 ????? ????? 1?0?2 ??210 200?1 22011 202?1 0011?

Allain (2002):
01??2 11??? 0??1? 00??? ????? ????? ????? ?1??0 ????

Novas *et al*. (2005):
2?100 0???? ????? ????? ????0 0?0?1 2112? 1?001 1?1?0 0???? ??0?2 ??202 00?12 20112 02?11 ????? ????? ????? ????? ????0 ???0? ?

SUPPLEMENTARY APPENDIX 5
HISTORICAL BIOGEOGRAPHIC ANALYSIS

A list of scored three-area statements based on the most parsimonious cladogram topology recovered by the present analysis. Three-area statements are scored under Assumption 1 of historical biogeographic studies, following the methods outlined in Nelson & Ladiges (1991) and Humphries & Parenti (1999).

Area	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Asia	0	0	0	0	0	0	0	0	0	?	?	0	0	?	?	?
Europe	1	?	?	1	1	1	1	1	1	1	1	?	?	?	0	0
N. Am	1	1	1	?	1	?	?	1	?	0	0	1	?	0	1	?
S. Am	?	1	?	1	?	?	1	?	?	1	?	1	1	1	1	1
Africa	?	?	1	?	?	1	?	?	1	?	1	?	1	1	?	1

Area	17	18	19	20	21	22	23	24	25	26	27
Asia	0	0	0	?	?	?	?	?	0	?	?
Europe	?	?	?	?	0	0	0	?	?	?	0
N. Am	1	1	?	0	1	1	?	1	?	0	?
S. Am	?	1	1	1	?	1	1	0	1	1	1
Africa	1	?	1	1	1	?	1	1	1	1	1

TABLES AND FIGURES

Table 1. A list of allosauroid terminal taxa used in this analysis, their geographic locations, and their temporal ranges (taken from Weishampel *et al*. 2004 and original descriptions).

Terminal Taxon	**Original Description**	**Location**	**Stratigraphic Age**	**Number of Species**
Acrocanthosaurus	Stovall & Langston 1950	North America	Early Cretaceous (Aptian-Albian)	1
Allosaurus	Marsh 1877	North America, Europe (Portugal)	Late Jurassic (Kimmeridgian-Tithonian)	3
Carcharodontosaurus	Depéret & Savornin 1927	Africa (Morocco, Niger)	Early Cretaceous (?Aptian, Albian-Cenomanian)	2
Giganotosaurus	Coria & Salgado 1995	South America (Argentina)	Early Cretaceous (?Albian-Cenomanian or ?Turonian)	1
Eocarcharia	Sereno & Brusatte in press	Africa (Niger)	Early Cretaceous (Aptian-Albian)	1
Mapusaurus	Coria & Currie 2006	South America (Argentina)	Early Cretaceous (Albian-Cenomanian)	1
Neovenator	Hutt *et al*. 1996	Europe (England)	Early Cretaceous (Barremian)	1
Sinraptor	Currie & Zhao 1993	Asia (China)	Middle-Late Jurassic (?Bathonian-Oxfordian)	2
Tyrannotitan	Novas *et al*. 2005	South America (Argentina)	Early Cretaceous (Aptian)	1

Table 2. A list of suprageneric allosauroid taxa and their shorthand definitions as employed in this paper. For more details, including a log of all published phylogenetic definitions for these and related taxa, see the file "Stem Archosauria" in the online database *TaxonSearch* (http://www.taxonsearch.org).

Taxon	**Definition**	**Definitional Author**
Allosauroidea	The most inclusive clade containing *Allosaurus fragilis*, but not *Passer domesticus*	Sereno (2005)
Allosauridae	The most inclusive clade containing *Allosaurus fragilis*, but not *Sinraptor dongi*, *Carcharodontosaurus saharicus*, or *Passer domesticus*	Sereno (2005)
Sinraptoridae	The most inclusive clade containing *Sinraptor dongi*, but not *Allosaurus fragilis*, *Carcharodontosaurus saharicus*, or *Passer domesticus*	Sereno (2005)
Carcharodontosauridae	The most inclusive clade containing *Carcharodontosaurus saharicus*, but not *Allosaurus fragilis*, *Sinraptor dongi*, or *Passer domesticus*	Sereno (2005)
Carcharodontosaurinae	The least inclusive clade containing *Carcharodontosaurus saharicus* and *Giganotosaurus carolinii*	New
Giganotosaurini	The most inclusive clade containing *Giganotosaurus carolinii*, but not *Carcharodontosaurus saharicus*	New

Table 3. Description of 12 recent allosauroid cladistic analyses, along with a quantification of shared data with the current study. Informative characters include those characters informative at the level of Allosauroidea (reduced to a common set of taxa shared with the present analysis: *Allosaurus*, *Acrocanthosaurus*, *Carcharodontosaurus*, *Giganotosaurus*, *Sinraptor*, and *Neovenator*). Shared characters refer to the number of characters in the current analysis also used by the previous analyses in question. Used characters refer to the number of informative characters in the previous analyses used in the current analysis. Scoring differences only include those differences that involve positive codings; a change to or from a missing datum ("?") is not included.

Analysis	**Allosauroid Taxa**	**Characters**	**Informative Characters**	**Shared Characters**	**Used Characters**	**Scoring Differences**
Sereno *et al*. 1996	5	63	11	10	9	0
Harris 1998	9	145	20	32	13	11
Forster 1999	4	99	25	21	15	7
Holtz 2000	7	386	52	42	22	29
Currie & Carpenter 2000	5	110	35	34	21	19
Azuma & Currie 2000	3	110	17	21	9	4
Allain 2002	5	45	13	12	8	2
Coria & Currie 2002	5	15	12	8	8	2
Rauhut 2003	5	224	9	23	5	2
Holtz *et al*. 2004	6	638	88	61	42	33
Novas *et al*. 2005	6	106	48	37	26	18
Coria & Currie 2006	6	110	46	35	22	20

This analysis	9	99	99	---	---	---

Table 4. Missing data in allosauroid terminal taxa. The percentage of missing data and the rank for each terminal relative to others (most complete ranked highest).

Taxon	**%**	**Rank**
Acrocanthosaurus	8	3
Allosaurus	0	1
Carcharodontosaurus	36	5
Giganotosaurus	24	4
Eocarcharia	69	8
Mapusaurus	52	7
Neovenator	44	6
Sinraptor	2	2
Tyrannotitan	80	9

Table 5. Comparison of stratigraphic consistency metrics for the current analysis (ingroup phylogeny only) and several alternative studies.

Analysis	**SCI**	**GER**	**MSM***	***p***	**RI_S**	**SD**
Full Analysis						
This Analysis	1.00	1.00	0.76	0.002	1.00	5
*Pruned to 5 Shared Taxa**						
This Analysis	1.00	1.00	0.73	0.05	0.71	2
Alternative 1	0.75	0.55	0.36	0.80	0.43	4
Alternative 2	0.75	0.66	0.36	0.43	0.57	3
Pruned to 6 Shared Taxa#						
This Analysis	1.00	1.00	0.75	0.007	0.75	3
Holtz 2000	0.80	0.84	0.51	0.05	0.67	4

Alternative 1 refers to the topology found in the analyses of Allain (2002) and Coria & Currie (2002), and Alternative 2 refers to the topology presented in Novas *et al*. (2005). Note that the topology presented by Novas et al. (2005) was not found in a reanalysis of their dataset. Abbreviations: SCI=Stratigraphic Consistency Index (Huelsenbeck 1994); GER=Gap Excess Ratio (Wills 1999); MSM*=modified Manhattan Stratigraphic Measure (Siddall 1998, Pol & Norell 2001); *p*=significance of the MSM* metric, describing the expected frequency of a better stratigraphic fit than that observed; RI_S=Retention Index of the Stratigraphic Character (Fisher 1992, Clyde & Fisher 1997); SD=Stratigraphic Debt, as calculated by a stratocladistic analysis (Fisher 1992) with five coded stratigraphic intervals (see Appendix 1). Each taxon was treated as a "point occurrence" for the GER and MSM, with absolute dates taken as the midpoint of the stage (or stages, depending on stratigraphic resolution) in which the taxon first appeared, based on the timescale of Gradstein *et al*. (2004). Due to imprecision in fossil dating, *Acrocanthosaurus*, *Carcharodontosaurus*, *Giganotosaurus*, and *Mapusaurus* were treated as temporally equivalent. For pruned stratocladistic analyses, stratigraphic character states not coded for any of the shared taxa were deleted. *=*Acrocanthosaurus*, *Allosaurus*, *Carcharodontosaurus*, *Giganotosaurus*, *Sinraptor*; #=the above plus *Neovenator*. *Tyrannotitan* was not included in the calculation of the comparative metrics for the pruned analyses, as its position in the present analysis is considered unstable.

FIGURE CAPTIONS

Figure 1: Sketal reconstruction of the Late Jurassic theropod *Allosaurus fragilis*, the best known member of Allosauroidea and one of the most common dinosaur discoveries in Upper Jurassic fossil deposits. (from Sereno 1999a)

Figure 2: Phylogenetic hypotheses for Allosauroidea advocated by 12 previous cladistic analyses (**A**-**K**) and a strict consensus of these topologies (**L**). Numbers next to clades in 2D,E,G, and J denote bootstrap support/Bremer support values. Support values for 2G refer to the analysis of Allain (2002) only.

Figure 3: Illustration of cladistic characters new to this study. **1**: Maxillae of *Sinraptor* (**a**), *Allosaurus* (**b**), and *Carcharodontosaurus* (**c**) in medial view; **2**: Dentaries of *Allosaurus* (**a**) and *Carcharodontosaurus* (**b**) in left lateral view; **3**: Dentaries of *Allosaurus* (**a**) and *Carcharodontosaurus* (**b**) in dorsal view; **4**: Premaxillae of *Allosaurus* (**a**) and *Neovenator* (**b**) in left lateral view; **5**: Squamosals of *Sinraptor* (**a**) and *Allosaurus* (**b**) in left lateral view; **6**: Gastralia of a generalized theropod (**a**) and *Carcharodontosaurus* (**b**) in dorsal view. Images 1a and 5a modified from Currie & Zhao 1993; 1b, 2a, 4a, and 5b from Madsen 1976; 4b from Hutt 1999; 6b from Stromer 1934. Numbers refer to character number in Appendix 1, and numbers in parentheses refer to character states. Scale bars equal 5 cm. No scale bars for 6a-b.

Figure 4: Illustration of cladistic characters new to this study. **1**: Ilia of *Allosaurus* (**a**) and *Mapusaurus* (**b**) in left lateral view; **2**: Ischia of *Sinraptor* (**a**) in left lateral view and *Allosaurus* (**b**) in medial view; **3**: Femora of *Allosaurus* (**a**) and *Carcharodontosaurus* (**b**) in cranial view; **4**: Tibiae of *Sinraptor* (**a**) and *Acrocanthosaurus* (**b**) in cranial view; **5**: Metacarpal 2 of *Allosaurus* (**a**,**c**) and *Acrocanthosaurus* (**b**,**d**) in lateral (**a**,**b**) and proximal (**c**,**d**) views. Images 1a, 3a, 5a, 5c modified from Madsen 1976; 1b from Coria & Currie 2006; 2a, 4a from Currie & Zhao 1993; 3b from Stromer 1931; 4b from Stovall & Langston 1950; 5 b, 5d from Currie & Carpenter 2000. Numbers refer to character number in Appendix 1, and numbers in parentheses refer to character states. Scale bars equal 5 cm. No scale bars for 3b, 4b.

Figure 5: Single most parsimonious cladogram recovered by the current analysis (99 characters in nine ingroup and four outgroup taxa). TL=171, CI=0.61, RI=0.70. Numbers next to clades denote boostrap support value/Bremer support value.

Figure 6: Cladogram recovered by rerunning the current analysis after the deletion of *Neovenator*.

Figure 7: Illustration of sources for new character codings. **A** and **B**: polymorphism in trigeminal nerve foramen morphology in *Carcharodontosaurus* (single, undivided foramen in *C. saharicus*, SGM-Din 1 [**A**] and incipiently-divided foramen in *C. iguidensis* [**B**]); **C**: strongly downturned paroccipital process in *Carcharodontosaurus* (*C.* n. sp.); **D**: broken suborbital flange on the postorbital of *Acrocanthosaurus* (OMNH 10146). Dashed lines represent broken bone surfaces. Abbreviations: **cn V**, trigeminal nerve; **fm**, foramen magnum; **pop**, paroccipital process; **sof**, suborbital flange. Scale bars in A and B equal 1 cm, and in C and D equal 5 cm.

Figure 8: Cladograms recovered by alternative published datasets when conflicting character state scores are changed to those favoured in the current analysis. **A**: Currie & Carpenter 2000; **B**: Allain 2002; **C**: Novas *et al*. 2005.

Figure 9: Cladograms recovered by alternative published datasets with the addition of *Neovenator*. **A**: Currie & Carpenter 2000; **B**: Allain 2002; **C**: Novas *et al*. 2005.

Figure 10: Stratigraphically calibrated phylogeny of Allosauroidea, based on the results of the current analysis. Thick lines indicate major ghost lineages, and thin lines reflect error in the temporal resolution of taxon occurrences (not true time ranges). Absolute dates for point occurrences are taken as the midpoint of the stage (or stages, depending on stratigraphic resolution) in which the taxon first appeared. All absolute dates based on the time scale of Gradstein *et al*. (2004).

Figure 11: Single most parsimonious cladogram recovered by three-area statement biogeographic analysis, based on the hypothesis of allosauroid phylogeny presented in this paper (TL=30, CI=0.90, RI=0.89).